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Acanthoecid choanoflagellates from the Atlantic Arctic Region – a baseline study

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Abstract

The examination and statistical analysis of loricate choanoflagellate material collected from Greenland waters during the period 1988–1998 represents a de facto baseline study of heterotrophic nanoflagellates from the Atlantic Arctic Region. The geographic sites sampled are Disko Bay (West Greenland) and the high-arctic North-East Water (NEW) and North Water (NOW) polynya. The analyses encompass close to 50 taxa. Some of these are described as new species, i.e. *Acanthocorbis glacialis*, *A. reticulata* and *Diaphanoeca dilatanda*. Two distinct clusters of species that are separated in time and space occur at all three sampling sites. A PCA analysis of NEW and NOW data points to that one community is linked to e.g. an early season high nutrient and low phytoplankton biomass scenario, whereas the other is predominant when nutrient levels are exhausted and the phytoplankton biomass high or declining. The material additionally allows for a comprehensive examination of e.g. the *Cosmoeca ventricosa* morphological variability encountered, as well as puts on record bimodal size variability within a number of species.

Keywords: Microbiology, Ecology

1. Introduction

Sustained changes in the Arctic Ocean and the Arctic sea ice cover have occurred over the last decades (see e.g. [Bijma et al., 2013](#)). The accelerated warming of high latitudes has led to that Arctic sea ice extent has declined throughout the year, with the largest reduction occurring in summer, and the Arctic Ocean is likely to become seasonally ice-free during this century. There is an increased stratification of ocean layers, coastal runoff has enlarged, ocean acidification has occurred, and winds and currents are prone for changes. These oceanographic impacts will have biological implications on the structure and function of high latitude ecosystems, modifying e.g. the magnitude, timing and spatial coverage of phytoplankton blooms and protist occurrences, and also likely lead to large scale range shifts of species and diversity issues at all trophic levels. The continued reduction of the sea ice extent will lead to irreversible ecosystem changes and diversity losses, because of the fine-tuned balance that evolution has established between pelagic and sea-ice associated communities (see e.g. [Hardge et al., 2017](#)). In the wake of these dramatic and on-going changes there is obviously a call for the publication of as many baseline studies as possible to provide reference data that can be used when revisiting Arctic habitats during the following decades. We are fortunate enough to have access to a large nanoflagellate data set compiled during the period 1988–1998 based on extensive light and transmission electron microscopical sampling from the high Arctic NEW ([Minnett et al., 1997](#)) and NOW ([Ingram et al., 2002](#)) polynya and from the subarctic Disko Bay on the Greenland west coast.

The loricate choanoflagellates is the target group selected for this baseline survey of high arctic and subarctic flagellate species diversity and community characteristics. Choanoflagellates are ubiquitous unicellular or colonial organisms that are present in all aquatic habitats where they often contribute significantly to microbial loop processes as grazers of bacteria-sized microorganisms. The protoplast is 3–5 μm long and carries a single anterior flagellum surrounded by a collar formed by numerous microvilli.

Recent molecular phylogenetic analyses have proved that the choanoflagellates is an ancestral sister group to the metazoa (e.g. [Snell et al., 2001](#); [Carr et al., 2008](#)). A thorough description of major aspects of choanoflagellate biology, ecology and evolution was recently provided by [Leadbeater \(2015\)](#). It is here evident that loricate choanoflagellate research has progressed substantially over the last decades with reference to e.g. functional morphology, ultrastructure and lorica construction, and based in particular on studies of cultured specimens. However, it is also apparent that there is a lack of progress in terms of elaborating patterns of global occurrence and understanding the underlying causal mechanisms.

There is at present consensus with respect to distributing choanoflagellate species among two distinct clades (Nitsche et al., 2011). The order Craspedida encompasses choanoflagellates with organic coverings only, whereas the Acanthoecida accommodates forms with siliceous loricae (loricate choanoflagellates) formed by meshworks of costal strips and ranging in size from 5- >100 μm . The elaboration of the lorica is used as the basis for species and genera delineation. The loricate choanoflagellates are almost exclusively found in marine environments within a salinity range from ca. 2 (e.g. the innermost parts of the Baltic Sea; Thomsen 1979) to >100 (in sea ice brine channels; Thomsen et al., 1997). The number of loricate choanoflagellates described is at present approx. 115. When adding known undescribed forms (Thomsen, unpublished results) it appears realistic that the maximum number of taxa is close to 150. The preliminary Tara Oceans survey (de Vargas et al., 2015) indicates that approx. 200 choanoflagellate OTU's (Operational Taxonomic Units) occur within the open ocean realms. This number also includes craspedid forms making the estimate above quite realistic.

While it is obvious that transmission (TEM) or scanning electron microscopy (SEM) of whole mounts of cells is the by far best technique when it comes to resolving lorica features (and the preferred tool when describing new taxa), it is possible with a high level of certainty to also analyse critical lorica features in e.g. air mounted material observed using a light microscope (LM) equipped with phase or Nomarski contrast oil-immersion lenses. This unique factor – a rarity among heterotrophic nano-sized flagellates – opens up for the possibility of using the loricate choanoflagellates as a proxy in the context of e.g. more basic studies on biodiversity and community ecology within heterotrophic flagellates at large. Our goals are here to provide updated accounts of species diversity and community analyses as well as surveying the morphological variability among individual species (primarily based on LM). This will eventually lead to an improved understanding of e.g. biogeographical issues (seasonal and spatial variability and their causes) of high importance in a climate change context, and also provide for the geographical region covered, the best possible morphotype reference framework for future DNA fingerprinting of further cold water adapted loricate choanoflagellate taxa.

Circumstantial evidence exists hinting at the existence of complex life-cycles among loricate choanoflagellates that pairwise link species currently allocated to separate genera (Thomsen and Østergaard, 2017). If the possibility of an interspecific switch between radically different morphotypes is indeed generic to loricate choanoflagellates, this will obviously have serious impact on future choanoflagellate taxonomy and nomenclature. While awaiting consolidating proof from e.g. nucleotide data (where different life-cycle morphotypes will consistently be shown to have the same sequence) it is thus important to emphasize that the morphotypes treated here as separate species may in fact rather be mutually

connected phases in complex life-cycles that are selected for by environmental triggers. Because there is likely to be a consistent link between environmental variables and specific morphotypes, it remains a valid approach to deal with loricate choanoflagellates as morphotypes in the context of 'species diversity' and succession. Describing new taxa (i.e. morphotypes) also remains a valid approach because we need, in the interim period while awaiting both a definitive confirmation of the existence of complex life-cycles and a complete mapping of these interrelationships, tools to distinguish and cross-reference the morphological diversity encountered at any specific locality. However, the longevity of any newly named species is unclear. It is pertinent here to draw a parallel to other groups of unicellular protists, i.e. the coccolithophores, which provide documentation of an alternation between haploid and diploid generations manifested through very distinct heteromorphic phases (Parke and Adams, 1960; Thomsen et al., 1991a, Billard, 1994). Efforts towards unveiling as many as possible of these heterococcolithophore (2n) –holococcolithophore (1n) life histories is still ongoing even though the general pattern was established decades ago. Likewise, it is to be expected that the quest among loricate choanoflagellates for life-cycle matches across the 'species' matrix will last for decades. Efforts to map the loricate choanoflagellate morphotype diversity across the complete range of habitats available to these organisms is crucial in the context of e.g. global change, and must be continued irrespective of that morphotype life -cycle links are searched for simultaneously.

2. Materials and methods

The Arctic material originates (Fig. 1) from the R/V 'Polarstern' ARK IX/3 North-East Water Polynya (NEW) cruise June-July 1993 and the R/V 'Pierre Radisson' North Water Polynya cruise (NOW) April-May 1998. Additional sampling of relevance here took place at the University of Copenhagen Arctic Station (Disko Bay, West Greenland) during the summers of 1988 (July-August), 1990 (August-September) and 1997 (June), and during early spring (April) in 1996.

The protocol for processing water samples for the light microscope (LM) and transmission electron microscope (TEM) was similar on all sampling occasions (see Moestrup and Thomsen, 1980). The nanoplankton community was concentrated for further processing by means of either centrifugation of a prefiltered (usually 20 µm) water sample (0.5–1 litre) or centrifugation of prefiltered material resuspended from an initial filtration of cells on top of e.g. a 1 µm Nuclepore filter. Small droplets of cells from the resuspended final pellet of material were placed on carbon coated grids for the TEM or on coverslips for the LM. Cells were subsequently fixed for ca. 30 seconds in the vapour from a 1–2% solution of OsO₄. After drying the grids were carefully rinsed in distilled water in order to remove salt crystals. Grids were shadow cast with either Au/Pd or Cr prior

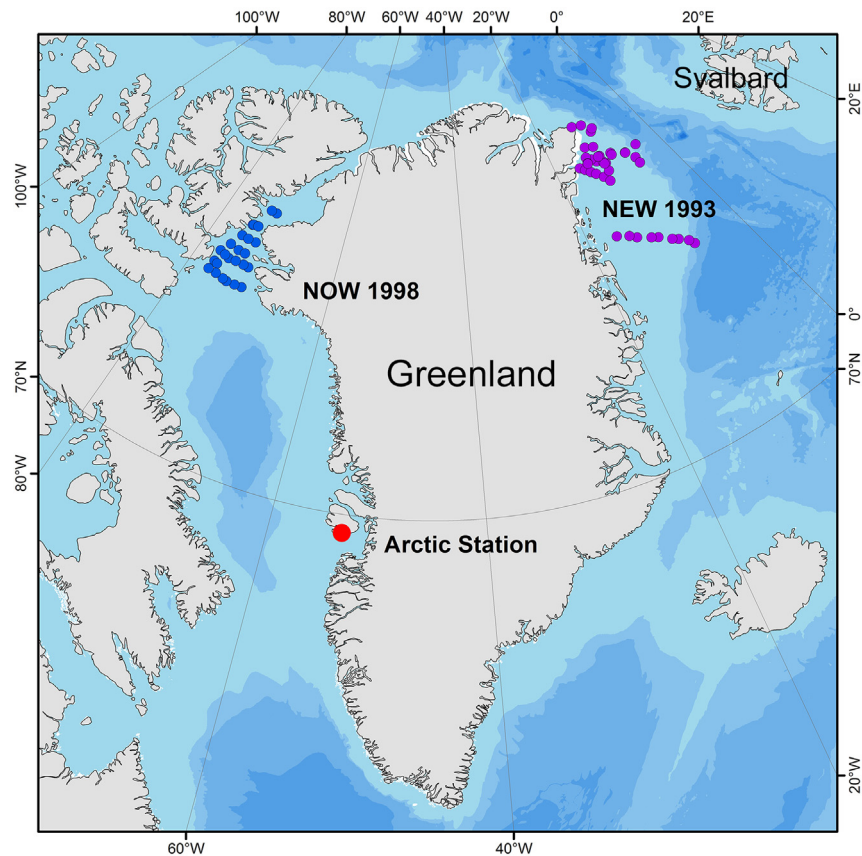


Fig. 1. Map of the sampling sites.

to the examination in JEOL electron microscopes property of the Botanical Institute at the Univ. of Copenhagen. Rinsed coverslips intended for LM were air-mounted upside down on a slide to render possible the use of oil-immersion lenses. The microscope used was an Olympus BH-2 equipped with phase contrast and an Olympus UC30 camera. The public domain software ImageJ ver. 1.50i was used for all measurements of cells. Community analyses (shade plots, PCA etc.) were conducted using the Primer v7 software package (Clarke et al., 2014).

The results presented here are based on the identification of approximately 35000 specimens. Author citations for all choanoflagellate species appear from Table 1.

3. Results and discussion

3.1. Previous investigations from the Atlantic Arctic region

Previous investigations on loricate choanoflagellates from the Atlantic Arctic Region are fairly numerous in particular when it comes to descriptions of new taxa, e.g. (Meunier, 1910; *Parvicorbicula* (*Corbicula*) *socialis*/Kara Sea), (Throndsen, 1970a; *Bicosta* (*Salpingoeca*) *spinifera*/Bear Island, Barents Sea), (Throndsen,

Table 1. Loricata choanoflagellate taxa recorded from Disko Bay, West Greenland (6 sampling events), the NEW and NOW polynya, and from neighbouring localities. A full author citation is provided to the extent possible within the space available.

Disko Bay, West Greenland								Polynya		Neighbouring localities		
	Thomsen, 1982	Hansen et al., 1989; Thomsen et al., 1995	Østergaard, 1993	Clausen et al., 1994	Thomsen, unpubl.	Thomsen, unpubl.		Northwater Polynya Thomsen, unpublished	NorthEast water Polynya Thomsen, unpublished	Daugbjerg et al., 1991 (Igloolik, Canada)	McKenzie et al., 1997 (Newfoundland, Canada)	Bérard-Therriault et al., 1999 (Gulf of St. Lawrence, Canada)
Material collected	20 July-6 Aug. 1977	1-11 Aug. 1988	20 Aug.-3 Sep. 1990	21 July-3 Aug. 1994	March 1996	16 June 1997	Additional recordings from Disko Bay (June 1972)	April-May 1998	June-July 1993	June-July 1989	1988-1992	1995-1997
Acanthocorbis apoda (Leadbeater, 1972) Hara and Takahashi, 1984	x	x								x		x
A. campanula(Espeland and Throndsen, 1986) Thomsen in Thomsen et al., 1991b		x	x									x
A. glacialis sp. nov.									x			
A. prolongata Thomsen in Thomsen et al., 1997					x			x				
A. reticulata sp. nov.			x									
A. unguiculata (Thomsen, 1973) Hara and Takahashi, 1984	x	x	x		x				x	x		x
Acanthoecca spectabilis Ellis, 1930	x						Leadbeater, 1979 (Manton pers. com.)					
Bicosta antennigera Moestrup, 1979	x	x	x	x	x	x	Manton et al., 1980	x	x	x	x	x
	x	x	x	x		x		x	x	x	x	x

(Continued)

(Continued)

Table 1. (Continued)

Disko Bay, West Greenland							Polynya		Neighbouring localities		
B. minor (Reynolds, 1976) Leadbeater, 1978							Manton et al., 1980				
B. spinifera (Throndsen, 1970a) Leadbeater, 1978	x	x	x	x	x	x	Manton et al., 1980	x	x	x	x
Calliacantha longicauda (Leadbeater, 1975) Leadbeater, 1978	x	x	x	x	x	x	Manton et al., 1975	x	x	x	x
C. natans (Grøntved, 1956) Leadbeater, 1978	x	x	x	x	x	x		x	x	x	x
C. simplex Manton and Oates, 1979	x	x	x	x	x	x		x	x	x	x
Conion groenlandicum Thomsen, 1982	x	x	x	x	x	x		x	x		x
Cosmoeca norvegica Thomsen in Thomsen and Boonruang, 1984	x ¹	x	x	x	x	x		x	x		
C. phuketensis Thomsen in Thomsen and Boonruang, 1984 cfr.									x		
C. takahashii Thomsen in Thomsen et al., 1990								x	x		
C. ventricosa Thomsen in Thomsen and Boonruang, 1984	x ²	x	x	x	x	x		x	x	x	x
C. ventricosa Thomsen and Boonruang, 1984 form A			x		x			x	x		x
C. ventricosa Thomsen and Boonruang, 1984 form C					x			x	x		

(Continued)

Table 1. (Continued)

Disko Bay, West Greenland						Polynya		Neighbouring localities		
C. ventricosa Thomsen and Boonruang, 1984				x		x	x			
E										
Crinolina aperta (Leadbeater, 1975) Thomsen, 1976	x	x	x		x		x		x	
C. isefjordensis Thomsen, 1976	x	x								x
Crucispina cruciformis (Leadbeater, 1974) Espeland and Throndsen, 1986										x
Diaphanoeca dilatanda sp. nov.			x							
D. grandis Ellis, 1930	x	x	x			x	x	x	x	x
D. multiannulata Buck, 1981	x	x		x	x	x	x			
D. pedicellata Leadbeater, 1972	x	x	x	x	x	x	x	x	x	x
D. sphaerica Thomsen, 1982	x			x		x	x	x		
D. undulata Thomsen, 1982	x	x	x	x		x	x	x		
Helgoeca nana (Thomsen, 1997) Leadbeater et al., 2008				x		x	x			
Monocosta fennica Thomsen, 1979			x							
Nannoeca minuta (Leadbeater, 1972) Thomsen, 1988	x ⁴	x		x						

(Continued)

Table 1. (Continued)

Disko Bay, West Greenland							Polynya		Neighbouring localities	
Parvicorbicula circularis Thomsen, 1976	x				x		x	x	x	x
P. manubriata Tong, 1997a				x			x	x	x	x
P. pachycostata Thomsen in Thomsen et al., 1997								x		
P. pedunculata Leadbeater, 1980								x	x	x
P. quadricostata Thronsen, 1970b	x	x	x	x	x	x	x	x	x	x
P. serrulata Leadbeater in Manton et al., 1975	x	x	x	x	x	x	x	x	x	
P. socialis (Meunier, 1910) Deflandre, 1960	x	x	x	x	x	x	Manton et al., 1976	x	x	x
P. superpositus Booth, 1990										x
Pleurasiga minima Thronsen, 1970b	x	x	x	x	x	x	Manton et al., 1976	x	x	x
P. reynoldsii Thronsen, 1970b	x	x	x	x		x	Manton et al., 1976	x	x	x
P. tricaudata Booth, 1990										x
Polyfibula caudata (Lead- beater, 1975) Manton et al., 1981syn. P. stipitata Manton et al., 1981	x ³	x	x			x				
P. sphyrelata (Thomsen, 1973) Manton et al., 1981										x
P. spp.	x	x	x					x	x	
	x									

Table 1. (Continued)

Disko Bay, West Greenland								Polynya		Neighbouring localities		
Saepicula leadbeateri Takahashi, 1981 cfr.												
Saroeca attenuata Thom- sen, 1979	x	x	x	x				x	x	x		
Spinoeca buckii Thomsen in Thomsen et al., 1995		x ⁵	x ⁵		x	x		x	x	x		
Stephanoeca aphe- lesThomsen in Thomsen et al., 1991b			x								x	
S. campanula (Kent, 1880) Boucaud-Camou, 1967			x								x	
S. cupula (Leadbeater, 1972) Thomsen, 1988		x ⁶										
S. diplocostata Ellis, 1930	x	x	x					x			x	x
S. diplocostata var. pau- cicostata Throndsen, 1969	x		x		x				x			
Number of taxa recorded	25	33	35	18	24	19	46(grand to- tal)	29	34	28	12	28

1) Choanoflagellate sp. 'N'; 2) Pleurasiga orculaeformis Schiller, 1925 sensu [Leadbeater, 1973](#); 3) Pleurasiga caudata; 4) Pleurasiga minuta; 5) Choano gen. et sp.nov. in [Hansen et al. 1989](#); 6) Pleurasiga cupula.

1970b; *Parvicorbicula quadricostata*, *Pleurasiga reynoldsii* and *P. minima*/Bear Island, Barents Sea), (Manton et al., 1975; *Polyfibula* (*Pleurasiga*) *caudata*, *Calliicantha* (*Salpingoeca*) *longicaudata*, *Parvicorbicula serrulata*, *Crinolina* (*Diaphanoeca*) *aperta*/West Greenland, Hudson Bay, Resolute Bay), (Reynolds, 1976; *Bicosta* (*Salpingoeca*) *minor*/Barents Sea), (Thomsen, 1982: *Conion groenlandicum*, *Diaphanoeca undulata*/West Greenland), and (Thomsen et al., 1995; *Spinoeca buckii*/West Greenland). The genus names in brackets refer to the name under which the organism was originally described.

Bursa (1961) reported on the occurrence of *Salpingoeca natans* and *Monosiga* sp. from Igloolik, arctic Canada. While the former was most likely a mixture of *Calliicantha* and *Bicosta* specimens (loc. cit. Fig. 17), the latter (loc. cit. Fig. 18) was a mixture of *Parvicorbicula socialis* and *Cosmoeca ventricosa* specimens. Manton and co-workers utilized material of arctic/sub-arctic origin (West Greenland, Hudson Bay, Resolute Bay, N. Alaska/Pt. Barrow) to expand on the morphological descriptions of previously described taxa, e.g. *Parvicorbicula socialis*, *P. quadricostata*, *Pleurasiga reynoldsii* and *P. minima* (Manton et al., 1976), *Calliicantha simplex* (Manton and Oates, 1979), *Bicosta minor*, *B. spinifera* and *B. antennigera* (Manton et al., 1980), and *Diaphanoeca grandis* (Manton et al., 1981).

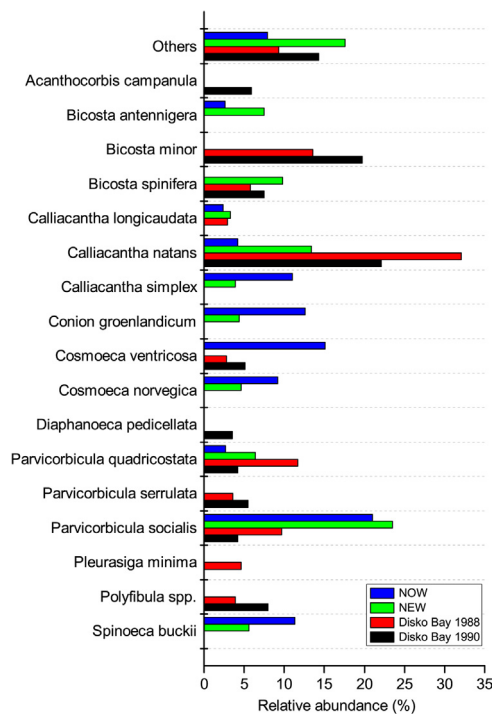


Fig. 2. Relative abundances of 'top-10' species from the polynya and two Disko Bay sampling seasons. Only three species, i.e. *Calliicantha natans*, *Parvicorbicula quadricostata* and *Parvicorbicula socialis* prevail at all four sites.

General surveys of the arctic/sub-arctic choanoflagellate fauna are, however, very limited but have been provided for West Greenland by [Thomsen \(1982\)](#) and [Thomsen et al. \(1995\)](#) and others exist in 'grey literature', e.g. [Hansen et al. \(1989\)](#) and [Clausen et al. \(1994\)](#).

3.2. Areas sampled

The high arctic polynya NEW and NOW ([Fig. 1](#)) were intensively studied during the 1990s as an integrated part of an international effort (IAPP, i.e. The International Arctic Polynya Project) to better understand, both in a contemporary and a historical perspective, the importance of these productive and ice-free high-arctic refugees (see e.g. [Deming et al., 2002](#); [Stirling, 1997](#)). Physical and biological features of these water bodies have been extensively accounted for in numerous publications and there is thus no need for an iteration of this information here (NEW: see e.g. [Schneider and Budéus, 1997](#); [Booth and Smith, 1997](#); [Von Quillfeldt, 1997](#)/NOW: see e.g. [Melling et al., 2001](#); [Lovejoy et al., 2002](#); [Odate et al., 2002](#); [Tremblay et al., 2002](#); [Vidussi et al., 2004](#)).

Disko Bay in West Greenland ([Fig. 1](#)/Arctic Station) has for decades remained a general marine research focus area (see e.g. [Nielsen and Hansen, 1995](#); [Levinson et al., 2000](#); [Hansen et al., 2003](#); [Munk et al., 2003](#); [Hansen et al., 2012](#)), both because these waters represent a significant resource for commercial fishing in Greenland (e.g. shrimps and halibut) but also because the Copenhagen University Arctic Station is located in Qeqertarsuaq on the south coast of the Disko Island. The general circulation pattern of the Disko Bay is cyclonic with coastal shelf water entering from the south ([Buch, 1990](#)). The pelagic system is much influenced by freshwater from glacier ice melt and sub-glacial freshwater flows. Seasonal sea ice coverage markedly impacts on the productivity of the system and seasonal succession of the plankton communities.

3.3. Regional and global diversity

[Table 1](#) summarizes findings of loricate choanoflagellates from West Greenland (Disko Bay), the arctic polynya (NEW, NOW), and neighbouring Canadian sites, i.e. Igloodik ([Daugbjerg et al., 1991](#)), Newfoundland ([McKenzie et al., 1997](#)) and Gulf of St. Lawrence ([Bérard-Therriault et al., 1999](#)). The communities analysed are characterized by similar numbers of species (roughly 20–30) with Newfoundland as the least diverse locality (12) and West Greenland (1988, 1990) as the most species rich single sites (>30). These numbers of total species occurrences are within the same range as those observed in e.g. Danish waters ([Thomsen et al., 2016](#)). The total number of species recorded from the Disko Bay area during a 20-year period of fairly intense sampling is close to 50. There is a considerable degree of similarity across the localities sampled both in terms of the actual species

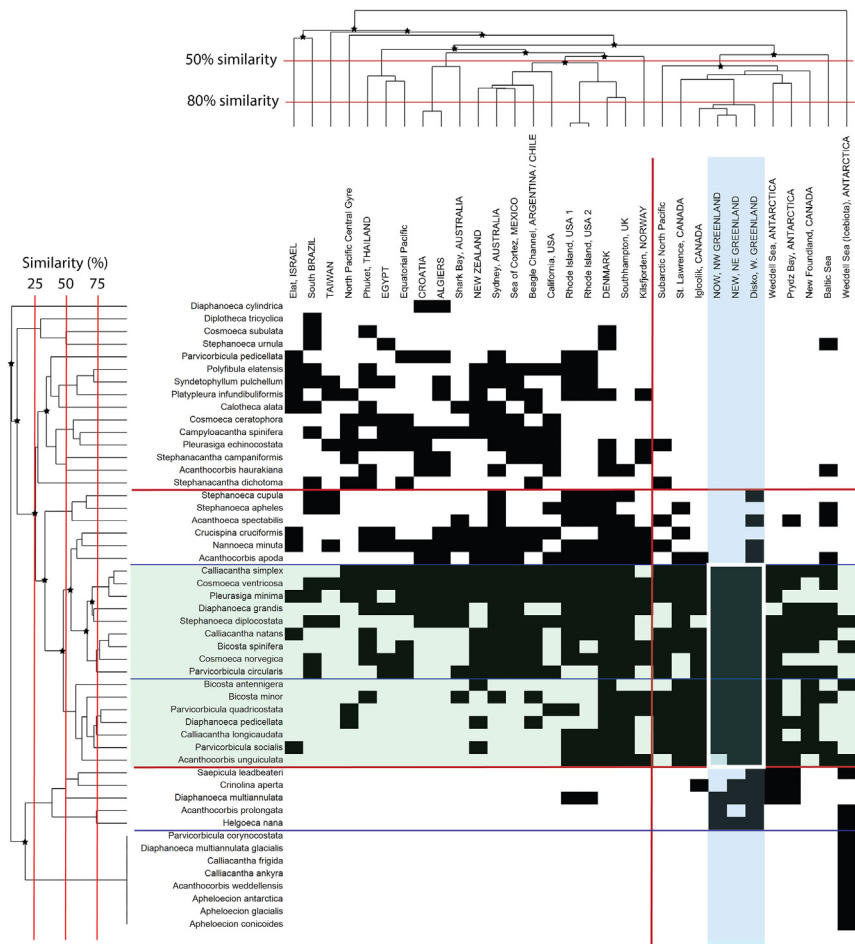


Fig. 3. Shade plot (Primer 7) showing global relationships among clusters of samples (31) and species (presence-absence data showing only the 50 most important taxa, as calculated by Primer7). Lines are added to the figure to support the interpretation. The star-shaped markers identify which nodes are statistically significant (1% level/Primer SIMPROF permutation test). The vertical line separates ‘cold’ water localities from ‘warm’ water localities. The NOW, NEW and Disko Bay samples cluster together (>80% similarity) and share a well-defined array of taxa (see inserted square). Data sources (1–31 from left to right): (1) Thomsen, 1978; (2) Bergesch et al., 2008; (3) Hara et al., 1997; (4) Hoepffner and Haas, 1990; (5) Thomsen and Boonruang, 1983a, b and subsequent papers; (7) Vørs et al., 1995; (8) Leadbeater, 1973; (9) Leadbeater, 1974; (10) Tong, 1997b; (11) Moestrup, 1979; (12) Tong et al., 1998; (15) Thomsen et al., 1991b; (16) Menezes, 2005; (18) Thomsen, 1992; (19) Tong 1997a; (20) Espeland and Throndsen 1986; (21) Booth 1990; (22) Bérard-Therriault et al., 1999; (23) Daugbjerg and Vørs, 1994; (24–26) this paper and Thomsen, 1982; Thomsen et al., 1995; (27) Thomsen et al., 1990, 1997; (28) Marchant and Perrin, 1990; (29) McKenzie et al., 1997; (30) Thomsen, 1979; (31) Thomsen et al., 1997; (6, 13, 14, 17) Thomsen unpublished.

recorded (Table 1) and their relative abundances (Fig. 2). The 10 most abundant species (17 species in total) observed in the NEW and NOW polynya and from Disko Bay during the summers of 1988 and 1990 are highlighted in Fig. 2. *Calliakantha natans*, *Parvicorbicula quadricostata* and *P. socialis* are the only

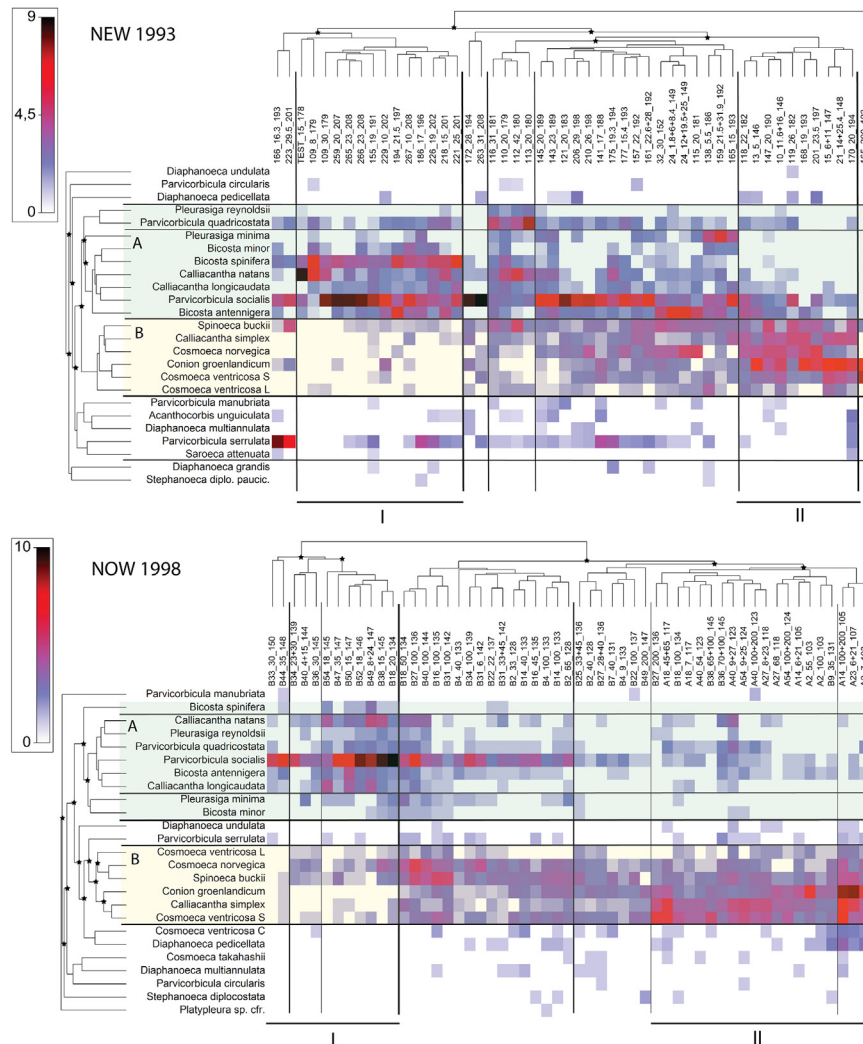


Fig. 4. Shade matrix plots (Primer 7) from NEW (top panel) and NOW (bottom panel). Samples (relative abundance data from 50 NEW stations and 55 NOW stations) and species (25 most important taxa) are clustered independently. Shading intensity within the matrix indicates the square root transformed relative abundance of each species (a legend is in the upper left of each plot). Both vertical and horizontal lines are added (thick and thin) to highlight different groups within the hierarchy and to help identify trends in the material. The star-shaped markers identify which nodes are statistically significant (1% level/Primer SIMPROF permutation test). Species clusters and groups of stations are further identified by letters (A-B and I-II). The individual samples are identified by station number, sampling depth(s) and Julian day, e.g. B33_30_150.

species that have peaked on all sampling occasions. Five species, i.e. *Bicosta antennigera*, *Calliicantha simplex*, *Conion groenlandicum*, *Cosmoeca norvegica* and *Spinioeca buckii* make it to the ‘top-10’ only at the high-arctic sites (NEW and NOW), whereas *Parvicorbicula serrulata* and *Polyfibula* spp. are Disko Bay dominants only.

Table 2. NEW, NOW and Disko Bay clusters of species (A, B) as defined by and extracted from the shade plots (Figs. 4, 6). Entries marked by lower case ‘x’ are those that fall slightly outside the core group of taxa in the analyses. Taxa not found at a specific site are left blank.

A	B	NEW	NOW	Disko Bay
Bicosta antennigera		X	X	
Bicosta minor		X	x	X
Bicosta spinifera		X	x	X
Calliakantha longicaudata		X	X	X
Calliakantha natans		X	X	X
	Calliakantha simplex	X	X	X
	Conion groenlandicum	X	X	X
	Cosmoeca norvegica	X	X	X
	Cosmoeca ventricosa L	X	X	X
	Cosmoeca ventricosa S	X	X	X
	Diaphanoeca pedicellata			X
	Spinoeca buckii	X	X	X
Parvicorbicula quadricostata		x	X	X
Pavicorbicula socialis		X	X	X
Plaurasiga minima		X	x	x
Pleurasiga reynoldsii		x	X	x

A global analysis of loricate choanoflagellate species diversity has been undertaken using presence/absence data from 31 sites. The shade plot (Fig. 3) includes only the most significant 50 taxa. The most diverging and unique loricate choanoflagellate community is that from the Weddell Sea ice biota (Thomsen et al., 1997). Beyond this there is a fairly distinct separation among ‘cold’ and ‘warm’ water stations (Fig. 3; vertical line). Within the ‘cold’ water node the Baltic Sea and also the Subarctic North Pacific communities are significantly separated from the remaining cluster of high latitude communities from both hemispheres, where the core groups are formed by Arctic (Igloodik, NOW, NEW, Disko Bay; similarity level >80%) and Antarctic communities (Weddell Sea, Prydz Bay) respectively. The latter representing an offshore and an inshore site differ at a similarity level of approx. 65%. A group of 16 taxa closely and significantly defines the geographic

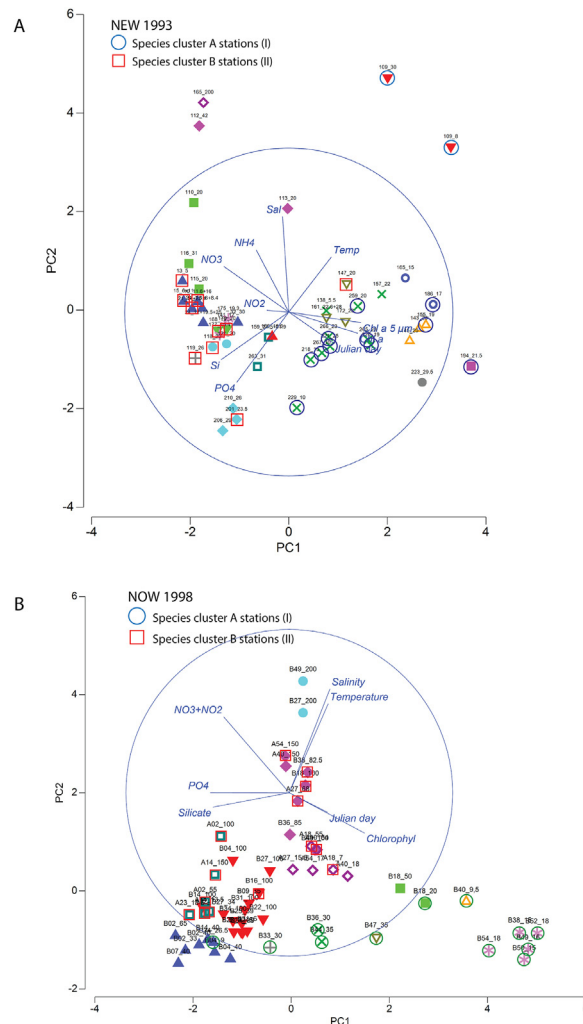


Fig. 5. PCA analyses of NEW (A) and NOW (B) environmental data (temperature, salinity, nutrients, phytoplankton biomass, and time). Species cluster A stations (I) and cluster B stations (II) are identified. The clusters A and B are evident from Fig. 4.

sites explored here (Fig. 3; white rectangle). This group of species is largely similar to that introduced in Fig. 2. When briefly browsing through the ‘warm’ water clusters it is similarly obvious that a natural and anticipated grouping of geographic sites occur within nodes that are statistically significant, such as a cluster of temperate North Atlantic sites, that geographically neighbour upon the arctic sites that are in focus here. Despite the clear signals that emanate from the global diversity analysis undertaken here (Fig. 3) it is obvious that there is still a critical difference in terms of coverage in time and space among the sites included which of course impacts on the robustness of the analysis. Sites such as Elat (Israel), south Brazil, and the North Pacific Central Gyre (Fig. 3, left hand side of the diagram) that are all characterized by low similarity levels are prone to relocate in the matrix once supplementary data becomes available. The most critical extrinsic

limitations when compiling species lists for biogeographical comparisons are under-sampling and under-reporting (Lee and Patterson, 1998).

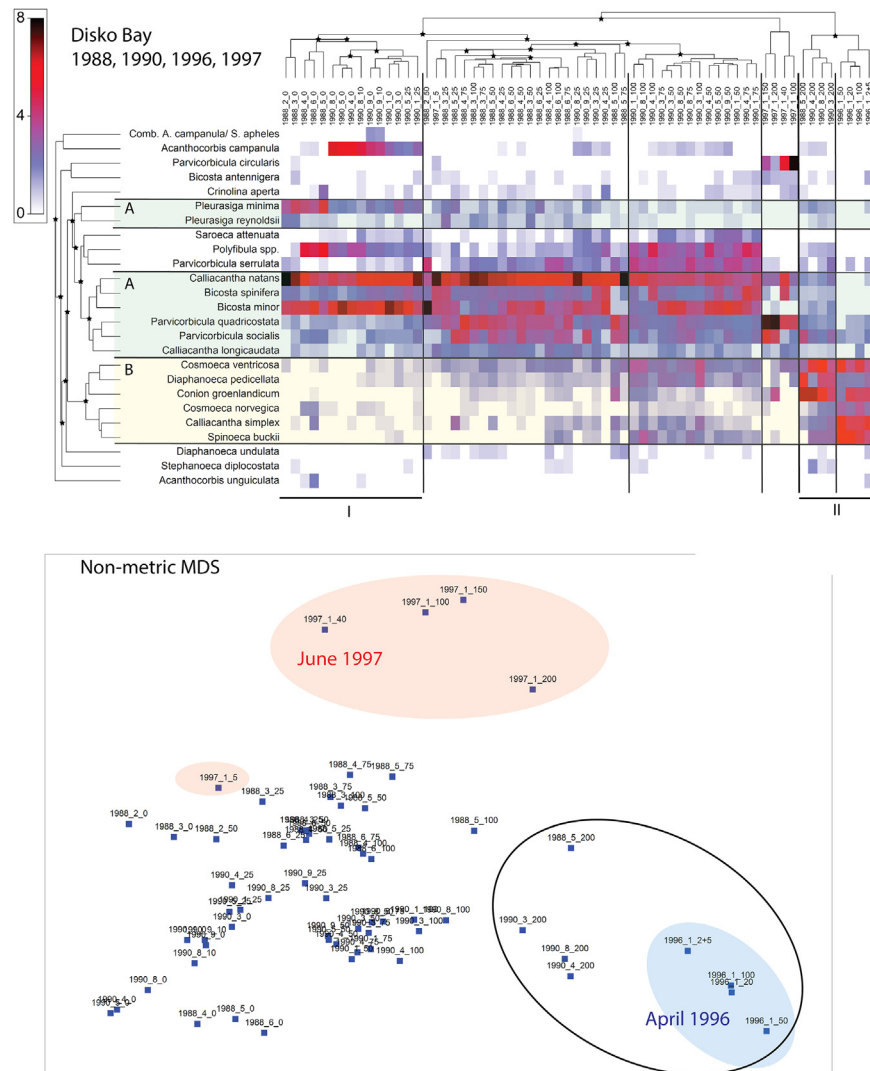


Fig. 6. Top: Shade matrix plot (Primer 7) of 63 Disko Bay samples (1988, 1990, 1996, 1997) and species (25 most important taxa). Shading intensity within the matrix indicates the square root transformed relative abundance of each species (a legend is in the upper left of the plot). Both vertical and horizontal lines are added (thick and thin) to highlight different groups within the hierarchy and to help identify trends in the material. The star-shaped markers identify which nodes are statistically significant (1% level/Primer SIMPROF permutation test). Species clusters and groups of stations are further identified by letters (A-B and I-II; cfr. Fig. 4). **Bottom:** Non-metric MDS plot of the same samples showing how samples from 1996 and 1997 as well as deep-water samples from 1988 and 1990 vary from the main cluster of samples. The individual samples are in both plots identified by year, station number, and sampling depth, e.g. 1990_1_100.

3.4. Community analyses

The NEW and NOW community analyses are conducted using the shade plot routine embedded in Primer v7. These visual displays (Fig. 4) are convincing in terms of aligning groups of samples with coherent clusters of species. Vertical and horizontal lines are used in the diagrams to help identify patterns of congruence. Both plots display quite some background ‘noise’, i.e. the apparent coincidental occurrence of species across a spectrum of stations that deviate in basic physical/chemical parameters and biological maturity (i.e. random natural variability within a complex system), but also some consistent patterns that are in fact mirrored across the NEW and NOW polynya sites. There are thus two statistically significant and almost identical species clusters (Fig. 4A, B and Table 2) that dominate within well-defined subsets of the stations sampled (Fig. 4I, II). Behind the obvious similarities between the NEW and NOW shade plots there are also noticeable differences in particular with respect to the occurrence patterns of the species clusters. Whereas the species groups A, B have in the NOW polynya little overlap in terms of co-occurrences at a subset of stations, the opposite trend applies

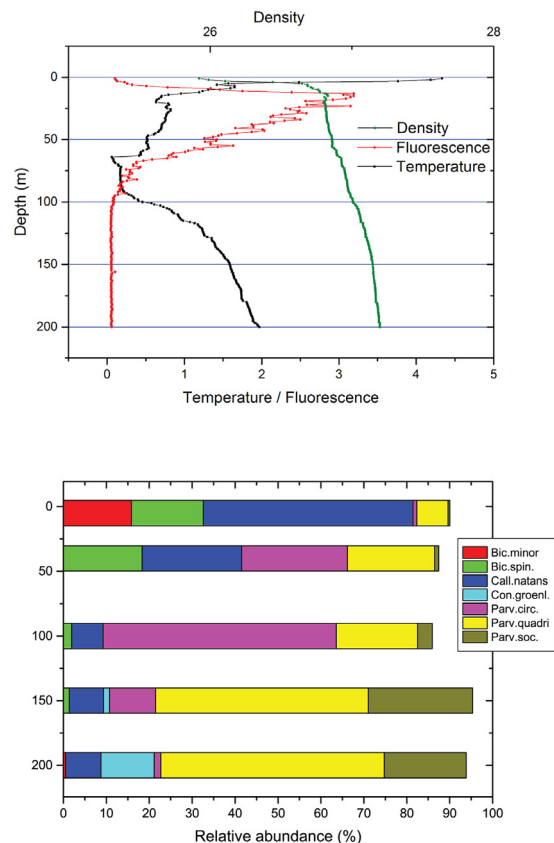


Fig. 7. Vertical structure (density (1000+ kg/m³), temperature (°C) and fluorescence (arbitrary unit)) of the Disko Bay water column (June 1997) at the Arctic Station permanent station (top), and water column distribution (relative abundance) of the most important taxa (bottom).

to the NEW polynya where a fairly extensive suite of stations are characterized by co-occurrences of the two species clusters.

In an attempt to elucidate the causes behind the patterns that emanate from the shade plot analyses, i.e. the robust links between species clusters (A, B) and specific subsets of samples (I, II), we have carried out (Fig. 5) an ordination of the NEW and NOW samples respectively (PCA analysis) based on a matrix of environmental variables (NEW: salinity, temperature, PO₄, NO₃, NO₂, NH₄, Si, total chl a, and chl a < 5 µm; NOW: salinity, temperature, PO₄, NO₃ + NO₂, Si, total chl). In both ordinations time (Julian day) was also included as a proxy for overall maturity of the systems sampled. Species cluster A stations (I) and B stations (II) are identified in the PCA plots (Fig. 5) and tend to cluster at either side of the panels (cluster A stations: right hand side of the panel/cluster B stations: left hand side of the panel). The PC1 axis (chlorophyll + Julian day versus nutrients) in both analyses thus partly separates the two clusters of samples. The PC1 explains 31.2% and 53.7% respectively in the NEW and NOW ordinations. When adding PC2 the percentages are increased to 53.7 and 78.1 respectively. In very general terms it appears justified to link the species cluster A with systems that are characterized by elevated to high phytoplankton biomasses and low nutrient levels, i.e. more mature systems that have passed through early successional stages. The cluster B species are on the contrary associated with a system in an early annual successional stage characterized by elevated nutrient levels and low phytoplankton biomasses.

The Disko Bay samples differ from the NEW and NOW samples in terms of geographic coverage. All stations visited are thus within a 20-km square. However, they have a much better coverage of depth strata and they also represent a decadal sampling effort. Despite these differences, it is intriguing that the species clusters A and B as derived from the analyses of NEW and NOW material, also significantly manifest themselves in the Disko Bay analysis (Fig. 6 top panel). Disko Bay oceanographic characteristics and annual trends in e.g. wind speed, ice cover, temperature, salinity and nutrients are thoroughly discussed by Hansen et al. (2012) based on repeated sampling during 1996–97 at the Arctic Station main station a few nautical miles south of Qeqertarsuaq at a depth of approximately 300 meters. A single vertical profile from this station is reproduced here as Fig. 7 (June 1997) showing CTD values and relative abundances of loricate choanoflagellates. The low salinity surface waters (upper 20–30 meters) consists of melt water and water that originates from the West Greenland current. An intermediate cold water layer (30–130 meters) is a consistent feature throughout a major part of the year and is likely derived from winter cooling and vertical convection of surface waters (Buch, 1990). The warmer bottom waters (below 150 meters) are fairly homogeneous throughout the year and comprise combinations of water of Atlantic origin and Arctic waters from the Baffin Bay Current with the latter component

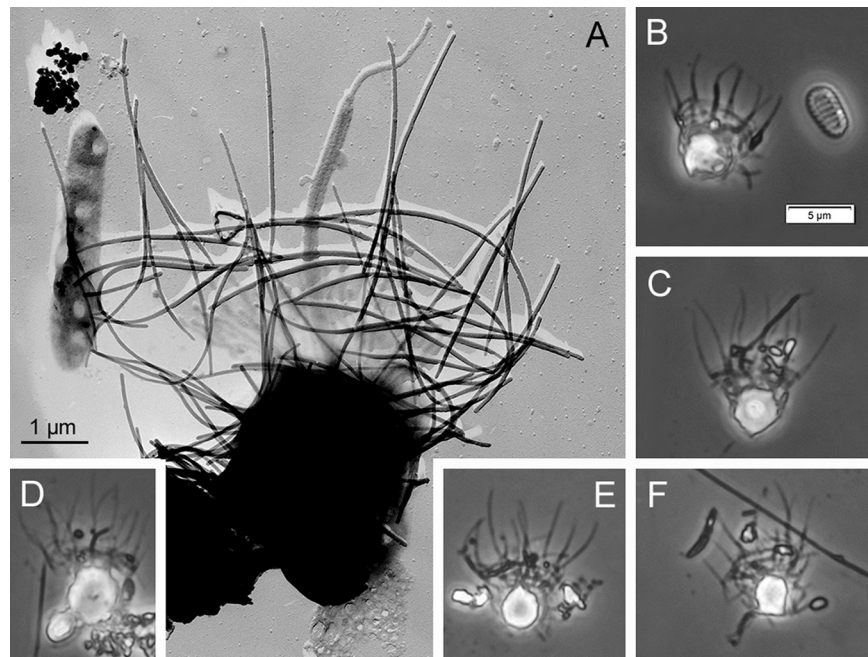


Fig. 8. *Helgoeca nana*. TEM (A) and LM micrographs (B-F) from NEW (A-C) and NOW (D-F). The scale bar (B) applies to all LM images.

usually being the dominant part. During the ice-free period the surface water (0–30 meters) major nutrients are completely depleted while persistently found at higher levels in the deeper parts of the water column. Considering these abiotic characteristics, it is not surprising when bearing in mind the findings from the polynya studies, that the cluster B species occur in deeper waters (most pronounced at the 200 meter stations sampled in 1990 but also evident from mid-range samples) and in samples from April 1996 (all depths sampled) collected during the ice-break period and prior to the onset of the spring bloom when nutrient levels are still high (Fig. 6). The cluster A species are predominant, in parallel with findings from the polynya, in surface waters deprived of nutrients corresponding to a mature ecosystem successional stage. The non-metric MDS plot (Fig. 6 lower panel) also clearly shows the link between in particular the deep-water samples and the samples from April 1996 characterized by a predominance of the cluster B species, and in addition highlights a possible major community change during 1997. All samples from June 1997 cluster separately with the single exception of the surface sample. The frequent occurrence in the June 1997 samples of *Parvicorbicula circularis* and to a lesser extent also *Bicosta antennigera* appear to be among the decisive factors that isolate this cluster of samples. It is interesting to take notice of that Hansen et al. (2012) report on an oceanographic regime shift during 1997 in Disko Bay starting in April of that year. It is tempting but also premature to link our observations here of a deviating community pattern for 1997 to these events.

(Continued)

Table 3. An overview of species allocation to the four lorica themes identified by [Leadbeater \(2015\)](#) with references to illustrations provided here. The * identifies genera that have been allocated to a theme with some degree of uncertainty.

Stephanoeca theme	Figures	Diaphanoeca/Crinolina theme	Figures
Acanthocorbis glacialis sp. nov.	Fig. 9F–J	Conion groenlandicum*	Fig. 13A–F
A. prolongata	Fig. 9K–O	Crinolina aperta	Fig. 11K–L
A. reticulata sp. nov.	Fig. 10A–D	Diaphanoeca dilatanda sp. nov.	Fig. 11F ; Fig. 12 (A–B, D–E)
A. unguiculata	Fig. 9A–E	D. grandis	Fig. 11A
Stephanoeca diplocostata var. paucicostata	Fig. 9P–Q, T	D. multiannulata	Fig. 11B–D
Stephanoeca sp.	Fig. 9R–S	D. multiannulata var. glacialis	Fig. 11J
		D. pedicellata	Fig. 11E ; Fig. 12C
		D. sphaerica	Fig. 11G
		D. undulata	Fig. 11H–I
Cosmoeca/Parvicorbicula-Pleurasiga theme	Figures	Bicosta/Calliacantha theme	Figures
Cosmoeca takahashii	Fig. 14G–H	Bicosta antennigera	Fig. 27A–L
C. ventricosa	Fig. 14I–K, M–Q	B. minor	Fig. 27M
C. ventricosa form A	Fig. 14A–F	B. spinifera	Fig. 27N
C. ventricosa form C	Fig. 14R–W	Calliacantha longicaudata	Fig. 28T–U
C. ventricosa form E	Fig. 14L, X–Ac	C. natans	Fig. 28N–S
Monocosta fennica*	Fig. 16F	C. simplex	Fig. 28A–F
Nannoeca minuta*	Fig. 25F–H ; Fig. 26A–B	C. simplex cfr.	Fig. 28G–M
Parvicorbicula circularis	Fig. 22A–H	Saroeca attenuata	Fig. 29A–F
P. manubriata	Fig. 17G–W ; Fig. 18A–B	Spinoeca buckii*	Fig. 30A–I
P. pedunculata	Fig. 24G		
P. quadricostata	Fig. 22I–S		

Table 3. (Continued)

Stephanoecca theme	Figures	Diaphanoeca/Crinolina theme	Figures
P. serrulata	Fig. 17X–Z; Fig. 21A–C		
P. socialis	Fig. 17A–F		
Pleurasiga minima	Fig. 25A–C		
P. reynoldsi	Fig. 25D–E		
Polyfibula caudata	Fig. 16A–E		

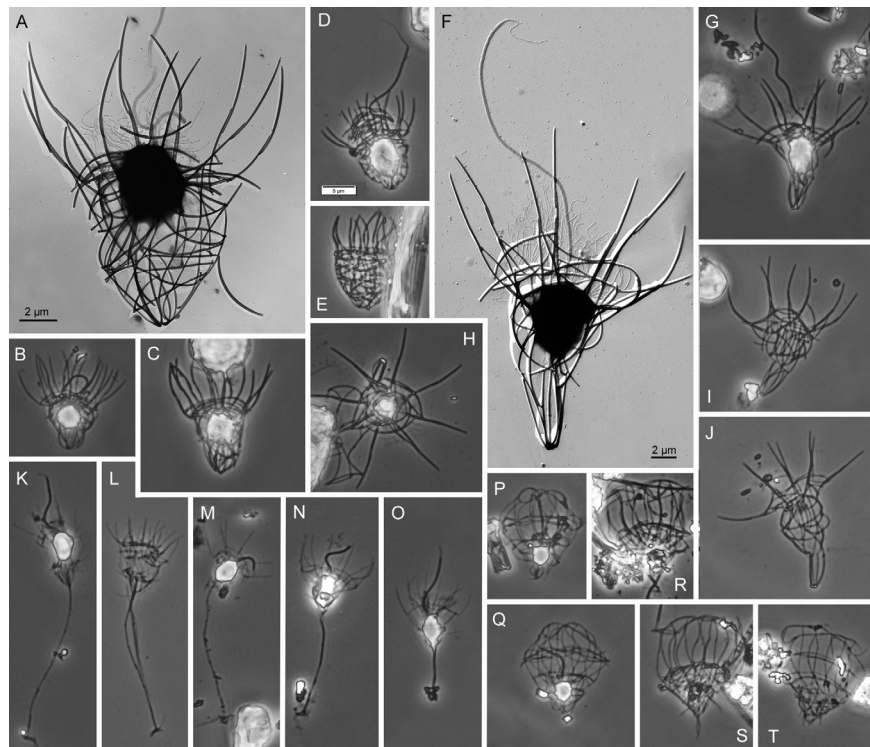


Fig. 9. *Acanthocorbis* spp. (A-O) and *Stephanoeca* spp. (P-T). *Acanthocorbis unguiculata* TEM (A) and LM images (B-E) from NEW (A-D) and Disko Bay (E); *Acanthocorbis glacialis* sp. nov. TEM (F) type micrograph and LM images (G-J) from NEW; *Acanthocorbis prolongata* LM images from Disko Bay (K-L), NEW (M, O) and NOW (N); *Stephanoeca diplocostata* var. *paucicostata* (LM) from NEW (P-Q) and NOW (T); *Stephanoeca ampulla* cfr. (LM) from NOW (R-S). The scale bar (D) applies to all LM images.

3.5. Species specific observations (Acanthoecida)

While a majority of the loricate choanoflagellate species encountered in Greenland waters (Table 1) are here fairly lavishly illustrated from LM (Fig. 8-9, 11, 13-14, 17, 22, 24-25, 27-28, 30), to actually constitute a field guide that will support future work on these organisms, the species specific general comments below are kept to a minimum, unless in places where we can add new information of relevance on morphological variability and autecology of a particular species. All LM images are shown at the same magnification (except Fig. 24G) to facilitate identification work.

3.5.1. Acanthoecidae (nudiform species)

Helgoeca nana (syn. *Acanthocorbis nana*) is a tiny species (Fig. 8) that typically occur in association with sea ice. Despite an overall resemblance to species of *Acanthocorbis*, to which genus it was originally ascribed (Thomsen et al., 1997), it has later been shown (Leadbeater et al., 2008) to be a nudiform species that is thus

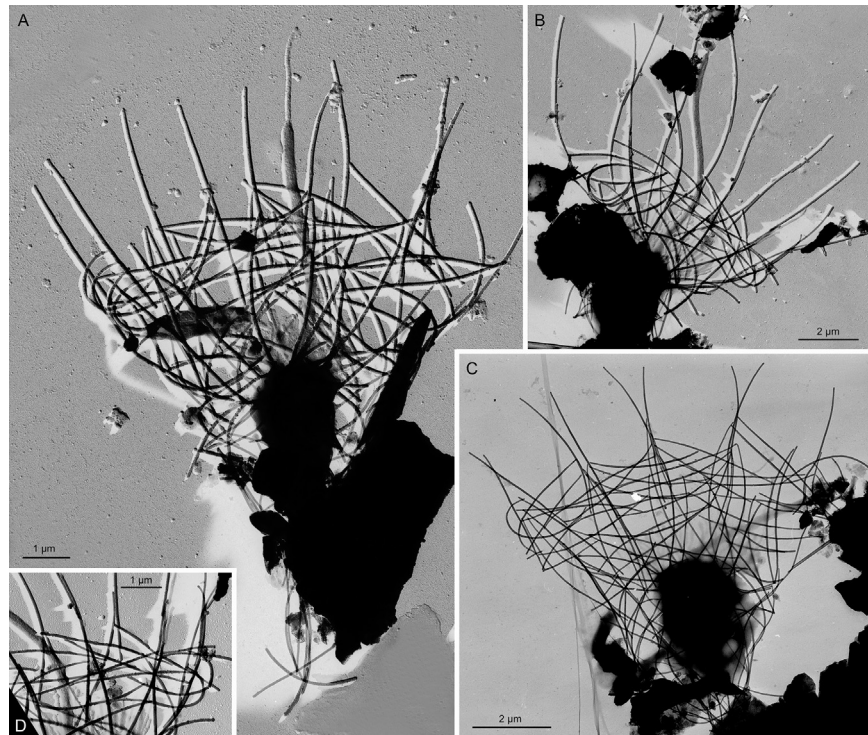


Fig. 10. *Acanthocorbis reticulata* sp. nov. TEM whole mounts (A-D) from Disko Bay 1990. Type micrograph (A).

phylogenetically clearly isolated from species of *Acanthocorbis*. Lorica size, the flaring nature of the longitudinal costae anteriorly and transverse costal strips encircling a major part of the flagellum (Fig. 8A) are critical features to look for in this species that are also adequately visible in LM (Fig. 8B-F).

3.5.2. *Stephanoecidae* (tectiform species)

Rather than dealing with the genera in alphabetical order, the taxonomic sections below are organized according to morphological themes as defined by Leadbeater (2015). A theme unites species and genera that share a basic costal pattern. The order in which the themes are arranged shows a progression from forms with small loricae comprising many costal strips to larger loricae with fewer costal strips. The same sequence also reflects a transition from coastal to oceanic forms. For the sake of simplicity Table 3 summarizes the allocation of species commented on below to a specific theme and also provides a link to illustrations provided here.

3.5.2.1. *Stephanoeca* theme

This theme (Figs. 9–10) unites the genera *Acanthocorbis* and *Stephanoeca*. Four species of *Acanthocorbis* have so far been encountered in Greenland waters and a handful of *Stephanoeca* species and morphotypes (Table 1).

3.5.2.1.1. *Acanthocorbis unguiculata*

(Fig. 9A–E) is infrequently observed in water column samples that are directly processed for analysis, whereas it is more commonly observed in either ice biota samples or in any kind of culture. The number of longitudinal costae and the robust and compact construction of the posterior lorica chamber are important diagnostic features. A claw-like termination of the anterior longitudinal costal strip is an important additional feature of this taxon when examined in the TEM. The tectiform mode of division in this species is evident from Fig. 9D.

3.5.2.1.2. *Acanthocorbis prolongata*

(Fig. 9K–O) was only observed in ice samples from the NOW polynya and Disko Bay. This species was originally described from the Antarctic ice biota (Thomsen et al., 1997) and has not been reported since then. Our material comprises cells that are, however, much reminiscent of the Antarctic specimens (see in particular Fig. 15 in Thomsen et al., 1997) in terms of lorica dimensions and structural features. Most important for a light microscopical recognition of this species is the number of longitudinal costae (8–10), two bands of transverse elements and the extended posterior pedicel (variable in length) which ends in a holdfast formed by a small cluster of costal strip. The holdfast is visible as a structural unit in LM. The Arctic specimens are all lightly silicified rendering a reproduction of lorica features suboptimal.

3.5.2.1.3. *Acanthocorbis glacialis*

3.5.2.1.3.1. Diagnosis

sp. nov. (Fig. 9F–J) Lorica conical, 20–25 μm long and with a diameter of ca. 10 μm at the level of the anterior transverse costa. The protoplast is located in the central part of the lorica and carries a flagellum that extends well above the anterior lorica rim. There are eight longitudinal costae that end in free diverging spines each exceeding the length of a single costal strip. The anteriormost tips are sharply pointed and occasionally claw-shaped. The penultimate anterior longitudinal costal strip is supported by 1–2 obliquely placed costal strips. Posteriorly the longitudinal costae form a handle-like element where the costal strips are arranged more or less in parallel. The posteriormost longitudinal costal strips, and to a lesser extent also the penultimate posterior longitudinal costal strips, are characterized by bended posterior tips which point inwards and form an anchoring disc for the lorica. Each longitudinal costa appears to comprise four costal strips. There is one well-defined anterior transverse costa and posterior to this additional transverse costal strip that form spiralling lorica elements. Division has not been observed. Based on an

overall similarity to species of *Acanthocorbis* it is expected that the new species is tectiform.

3.5.2.1.3.2. Type specimen

Fig. 9F found in a brine sample collected by hose from a 1 meter deep hole drilled into multi-year ice on 22 July 1993 at the approximate position 80°11.18 N and 16°15.12 W (NEW polynya).

3.5.2.1.3.3. Etymology

The species epithet is chosen to reflect the preferred biota for this organism. The pivotal features of the new taxon are the number of longitudinal costae (typically 8), the handle-like appearance of the posterior tier of longitudinal costal strips, and the hook-shaped termination of the posterior longitudinal costal strips. *Acanthocorbis glacialis* bears a resemblance to e.g. specimens of *A. unguiculata* in which the posterior part of the lorica is less robustly developed than typical for the species

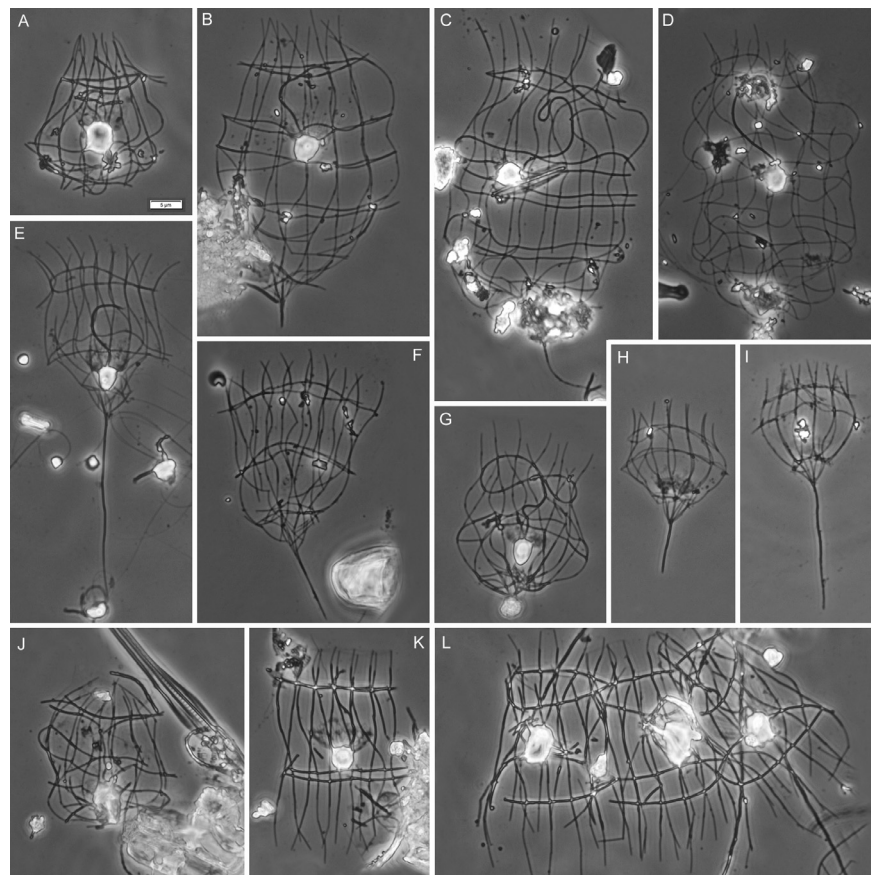


Fig. 11. *Diaphanoeca* spp. and *Crinolina aperta* (LM). *Diaphanoeca grandis* from NEW (A); *Diaphanoeca multiannulata* from NEW (B), NOW (C) and Disko Bay (D); *Diaphanoeca pedicellata* from NEW (E); *Diaphanoeca dilatanda* sp. nov. from Disko Bay (F); *Diaphanoeca sphaerica* from NEW (G); *Diaphanoeca undulata* from NOW (H-I); *Diaphanoeca multiannulata* var. *glacialis* from NEW (J); *Crinolina aperta* (K-L) from Disko Bay, June 1997. The scale bar (A) applies to all LM images.

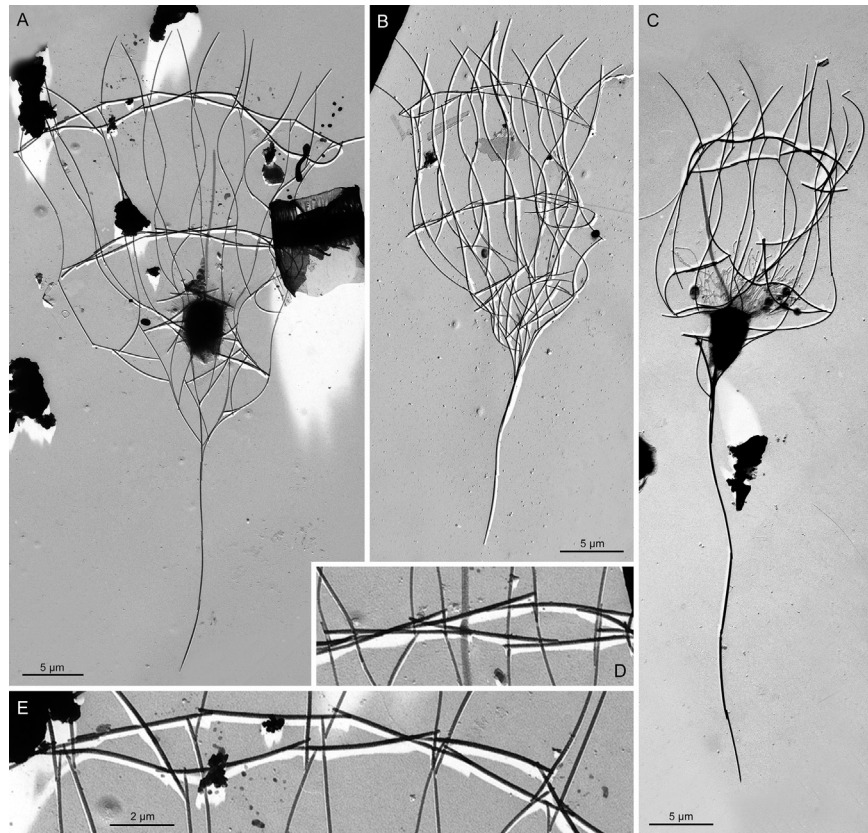


Fig. 12. TEM whole mounts of cells from Disko Bay. *Diaphanoeca dilatanda* sp. nov. (A-B, D-E; type micrograph (A)) and *D. pedicellata* (C). The scale bar (E) also applies to D.

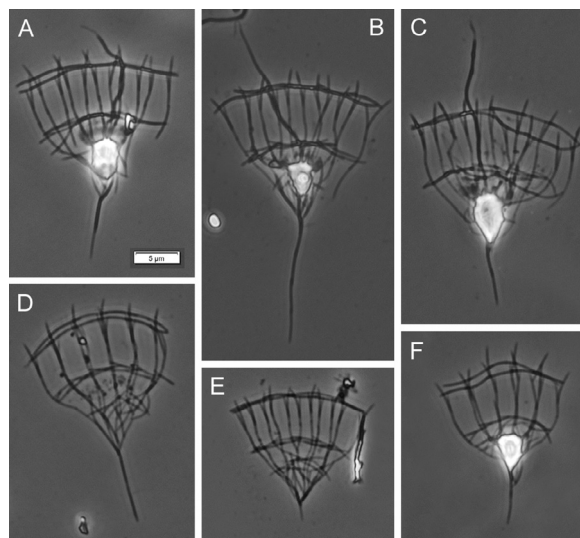


Fig. 13. *Conion groenlandicum* from NEW (A-B), NOW (C) and Disko Bay (D-F). The scale bar (A) applies to all LM images.

(see e.g. Fig. 9B–C). However, the number of longitudinal costae still clearly separates these species. The new species is tightly linked with habitats associated to sea ice.

3.5.2.1.4. *Acanthocorbis reticulata*

3.5.2.1.4.1. Diagnosis

sp. nov. (Fig. 10A–D) Lorica conical, ca. 10 μm long and with a diameter of 5 μm at the level of the anterior transverse costa. Approximately 10 (9–11) longitudinal costae that project anteriorly as free spines that are shorter than one costal strip. Posteriorly the longitudinal costae join to form a short stalk that in turn is terminated by some irregularly positioned costal strips forming a holdfast. Spiralling transverse costae are fairly evenly distributed over the entire lorica with denser sections anteriorly and posteriorly. At the anterior end each transverse costal strip spans the distance between three longitudinal costae and they are placed with a constant distance between the shifted neighbouring strips. Division has not been observed. Based on an overall similarity to species of *Acanthocorbis* it is expected that the new species is tectiform.

3.5.2.1.4.2. Type specimen

A collected (Fig. 10) at #8 (Disko Bay, south of Brededal/69°15.39 N 53°05.40W) from a depth of 75 m on 30 August 1990.

3.5.2.1.4.3. Etymology

‘reticulata’ (L) means mesh-like and refers to the appearance of the lorica walls.

Acanthocorbis reticulata bears some resemblance to in particular *A. unguiculata* and *A. glacialis* which basically justifies the inclusion of this new taxon in the genus *Acanthocorbis*. The species has so far only been observed in samples from Disko Bay and only during 1990 field work. A total of 21 individuals were found (TEM: 8; LM: 13) and the vast majority of these occurred at depths between 50 and 100 meters.

A few examples of *Stephanoeca* loricae as they appear from LM preparations are shown in Fig. 9P–T. *Stephanoeca diplocostata* var. *paucicostata* (Fig. 9P–Q, T) is frequently observed from ice related habitats. The second species illustrated (Fig. 9R–S) is reminiscent of both *S. ampulla* (Ellis, 1930) and *S. campanula* (Boucaud-Camou, 1967).

3.5.2.2. *Diaphanoeca/Crinolina theme*

Species allocated (Figs. Fig. 11, Fig. 12, Fig. 13) to this group possess spacious loricae that are either closed posteriorly (*Diaphanoeca*) or open (*Crinolina*). The lorica is often constricted at the anterior end, and the longitudinal costae terminate as free spines. The protoplast is suspended from either the first or the second

transverse costa counted from the anterior cell end. The genus *Conion* is tentatively allocated to this group of species. The costal strip pattern of junctions between transverse and longitudinal strips is at the anterior lorica end much like that observed in e.g. species of *Diaphanoeca*.

The genus *Diaphanoeca* is represented in Greenlandic waters by 6 taxa which are all illustrated here from LM, i.e. *D. grandis* (Fig. 11A), *D. multiannulata* (Fig. 11B–D), *D. pedicellata* (Fig. 11E), *D. dilatanda* sp. nov. (Fig. 11 F), *D. sphaerica* (Fig. 11G) and *D. undulata* (Fig. 11H–I). *Diaphanoeca multiannulata* was initially described from the Weddell Sea, Antarctica (Buck, 1981), and has since then been found to be abundantly present in Antarctic pelagic habitats (e.g. Thomsen et al., 1990; Thomsen et al., 1997). For some time both this species and also *Cosmoeca takahashii* (see further below) were de facto signature species for the Antarctic heterotrophic nanoflagellate community and furthermore considered to be most likely endemic to the circum-Antarctic water masses. However, as is evident from Table 1, *D. multiannulata* has been regularly recorded from Disko Bay, West Greenland, since 1988 and was also found to be present in both polynya. The Arctic material comprises cells that are indistinguishable from southern hemisphere specimens (Thomsen et al., 1990). Numerical characteristics of *D. multiannulata* from Disko Bay (n = 19) are as follows: lorica length 37–52 µm (mean value 44.8); lorica maximum diameter 14–17 µm; distance (mean values) between successive transverse costae (from the anterior end): 13/7.3/8.5/5.3 µm; number of longitudinal costae 11–13; number of transverse costae 4–5. *Diaphanoeca multiannulata* has so far not been found outside the polar regions. When examining ice biota samples from the NEW polynya specimens identical to *D. multiannulata* var. *glacialis* as described from Antarctic ice samples (Thomsen et al., 1997) were also encountered (Fig. 11 J). The genus *Diaphanoeca* is a keystone genus in northern latitude cold waters as evidenced by a significant species diversity, and accommodates beyond the species documented here from Greenland waters only two additional species studied by means of transmission electron microscopy, i.e. *D. cylindrica* Leadbeater from the Mediterranean (Leadbeater, 1974), and *D. spiralifurca* Hara from Japanese and Taiwanese coastal waters (Hara et al., 1996). *Diaphanoeca fiordensis* (Scagel and Stein)Norris is only known from a drawing based on a light microscopical analysis of material from a Canadian British Columbian fjord system (Scagel and Stein, 1961). The exact identity of this organism remains unclear. When considering the size of the lorica and features such as the narrow anterior opening it appears most likely that this species should be relegated to a *D. grandis* synonym.

3.5.2.2.1. *Diaphanoeca dilatanda*

3.5.2.2.1.1. Diagnosis

sp. nov. (Fig. 11F, Fig. 12A–B, D–E) Protoplast ca. $5 \times 3 \mu\text{m}$ and situated posteriorly in a broadly conical lorica chamber formed by 15–16 longitudinal costae and 3 transverse costae. The lorica chamber is 30–35 μm long and with a diameter at the level of the anterior and middle transverse costae corresponding to ca. 18 and 14 μm respectively. Each longitudinal costa comprises 6 costal strips. The anteriormost longitudinal costal strips project as free spines. The middle transverse costa is at the level of the junctions between the third and fourth longitudinal costal strips counted from the anterior lorica end. The posterior transverse costa is less well defined creating together with the amalgamating longitudinal costal strips a somewhat irregular mesh of costal strips that eventually leads into a posterior stalk.

3.5.2.2.1.2. Type specimen

Fig. 12A collected at #5 (Disko Bay, south of Torskenaes/69°14.6 N 53°37.36W) from a depth of 50 m on 25 August 1990.

3.5.2.2.1.3. Etymology

‘dilatanda’ (from Latin ‘dilatandus’) = widen; refers to the longitudinal costae that diverge significantly at the anterior lorica opening.

The new species, *D. dilatanda*, resembles most closely *D. pedicellata* (Fig. 11E, 12C) (Leadbeater, 1972). The diagnostic features distinguishing the two taxa are the addition of an additional strip to each of the longitudinal costae (which causes the lorica chamber to be slightly larger in *D. dilatanda*), and the fact that there is not in *D. dilatanda* a constriction in width at the level of the anterior transverse costa. As is evident from Fig. 11 a constriction in diameter at the level of the anterior transverse costa is otherwise a shared feature across all *Diaphanoeca* species encountered in Greenlandic waters. Changes in lorica diameter is simply controlled by the degree of overlap between neighbouring transverse costal strips. It is evident that these overlaps are indeed very narrow in the *D. dilatanda* anterior transverse costa (Fig. 12E) in comparison with what is typical for the middle transverse costa (Fig. 12D).

Diaphanoeca dilatanda has so far only been found in samples from Disko bay collected during 1990 (Fig. 12A–B, D–E) and 1996 (Fig. 11F). There is a good chance that Antarctic material examined by Buck (1981) and tentatively described under the heading *Acanthocorbis spiculifera* Norris may in fact be conspecific with the Arctic species *D. dilatanda* described here. The Weddell Sea specimen has 16 longitudinal costae, three transverse costae, and a lorica height of approx. 25 μm .

Two species of *Crinolina*, i.e. *C. aperta* and *C. isefjordensis*, are reported from Greenlandic waters (Table 1). Whereas the latter species is infrequently observed and so far, best documented in Thomsen, 1982 (loc. cit. Fig. 35), *C. aperta* (Fig. 11K–L) is more commonly observed and sometimes seen to form small to large colonies where neighbouring cells unite along the longitudinal costae,

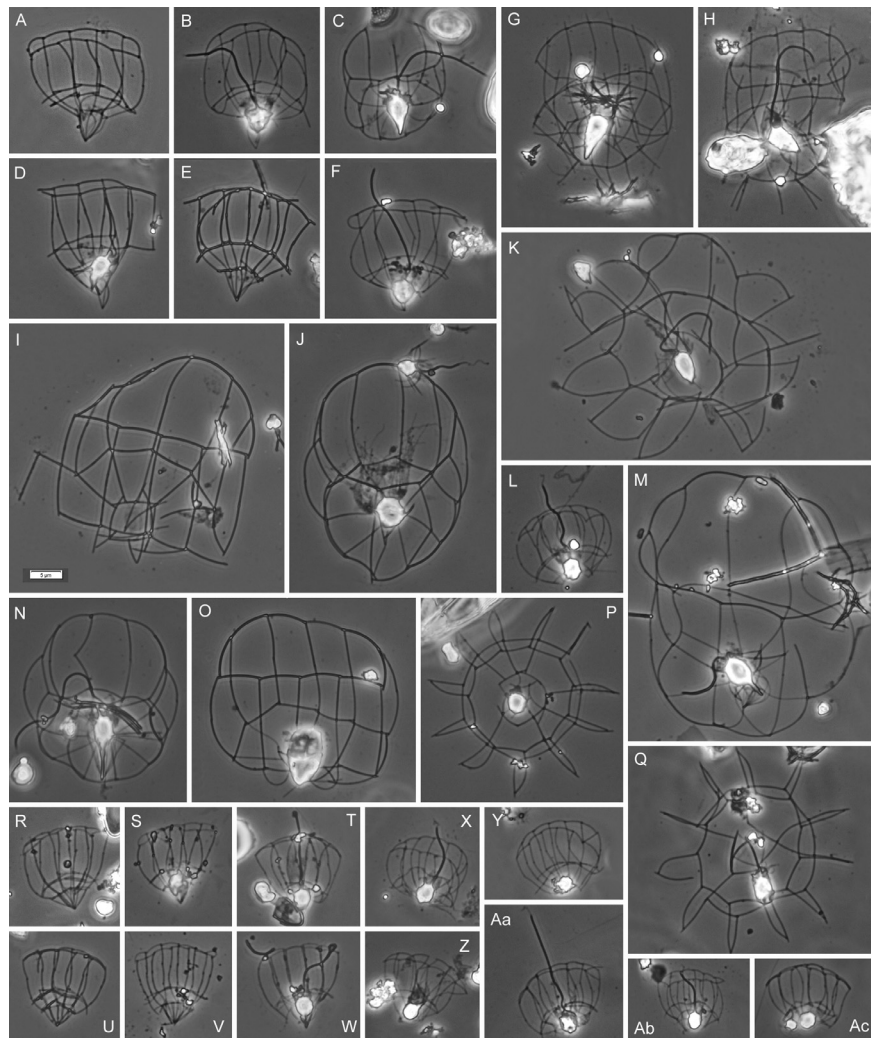


Fig. 14. *Cosmoeca* spp. (LM) *Cosmoeca ventricosa* morphotypes (A-F, I-Ac) and *Cosmoeca takahashii* from NOW (G-H). *C. ventricosa* form A with 9 long. costae and small lorica (A-F) from NOW (A-C), Disko Bay (D-E) and NEW (F); *C. ventricosa* with 9-11(12) long. costae and large lorica (I-K, M-Q) from NOW (I, K, N), Disko Bay (M, O-P) and NEW (J); *C. ventricosa* form E with 12 long. costae and small lorica (L, X-Ac) from NOW (Aa, L, X-Z), Disko Bay (Ac) and NEW (Ab); *C. ventricosa* form C with 10 long. costae and small conical lorica (R-W) from NOW (R, W), Disko Bay (S, U-V) and NEW (T). The scale bar (I) applies to all LM images.

forming curved and convex colonial plates. This is similar to what is known from *Diaphanoeca sphaerica* (Thomsen, 1982).

3.5.2.2.2. Conion groenlandicum

(Fig. 13A–F) was first described from West Greenland (Thomsen, 1982) and has since then become established as an Arctic keystone species. It shares basic features with species of *Diaphanoeca* in particular with reference to the anterior

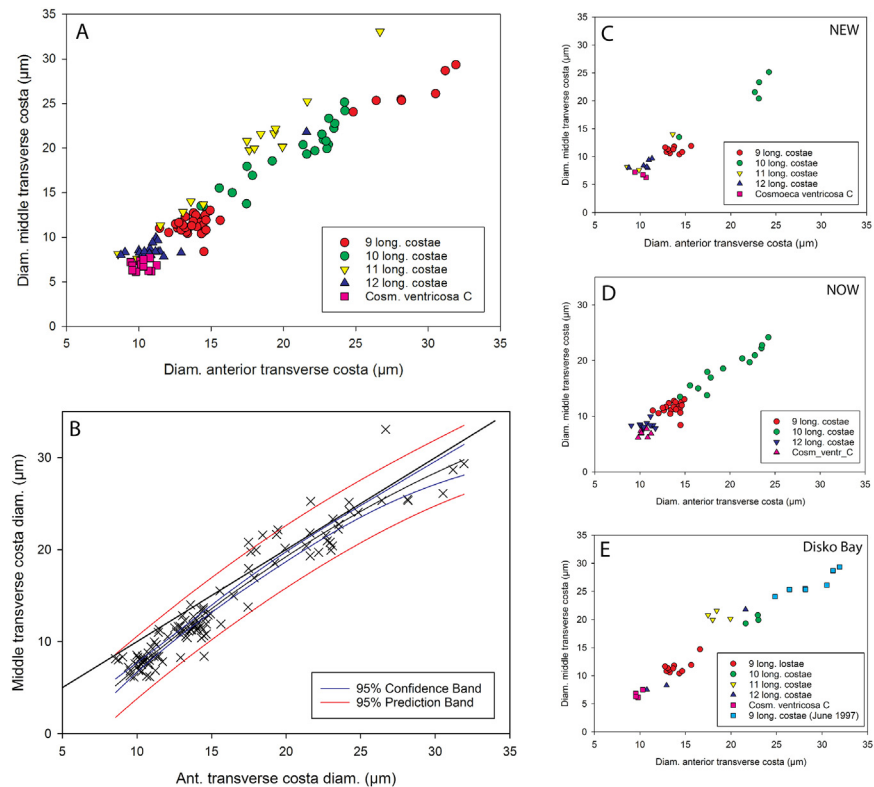


Fig. 15. *Cosmoeca ventricosa* morphotypes; pooled material from Greenland showing (A) the size variability (anterior and middle transverse costa diameter) across ranges in number of longitudinal costae. Small lorica forms with 12 and 9 long. costae cluster densely as do also the *C. ventricosa* form C specimens. (B) Diagram highlighting the size variability in transverse anterior and transverse middle costa diameter. A non-linear regression ($R = 0.9614$) with confidence and prediction bands is fitted to the data point. The black line represents the situation where the two costae are of the same size. (C-E) Site specific occurrences of the various morphotypes of *Cosmoeca ventricosa*.

lorica end costal strip patterns (Thomsen, 1982). Yet it is easily distinguished also from LM because of the conical lorica shape and modest dimensions (lorica chamber height: 10–15 μm).

3.5.2.3. *Cosmoeca/Parvicorbicula-Pleurasiga* theme

The uniting features (Figs. 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26) are here a funnel- or barrel-shaped lorica comprising relatively few costal strips arranged in 1–3 transverse costae, and a variable number of longitudinal costae (4–15) comprising 3–4 costal strips each. The protoplast is posteriorly located and the lorica is in most cases terminated by a transverse costa anteriorly.

3.5.2.3.1. *Cosmoeca*

Thomsen in Thomsen and Boonruang, 1984 (Fig. 14). A standard *Cosmoeca* lorica comprises a fairly large number of longitudinal costae (9–12; each composed of 4

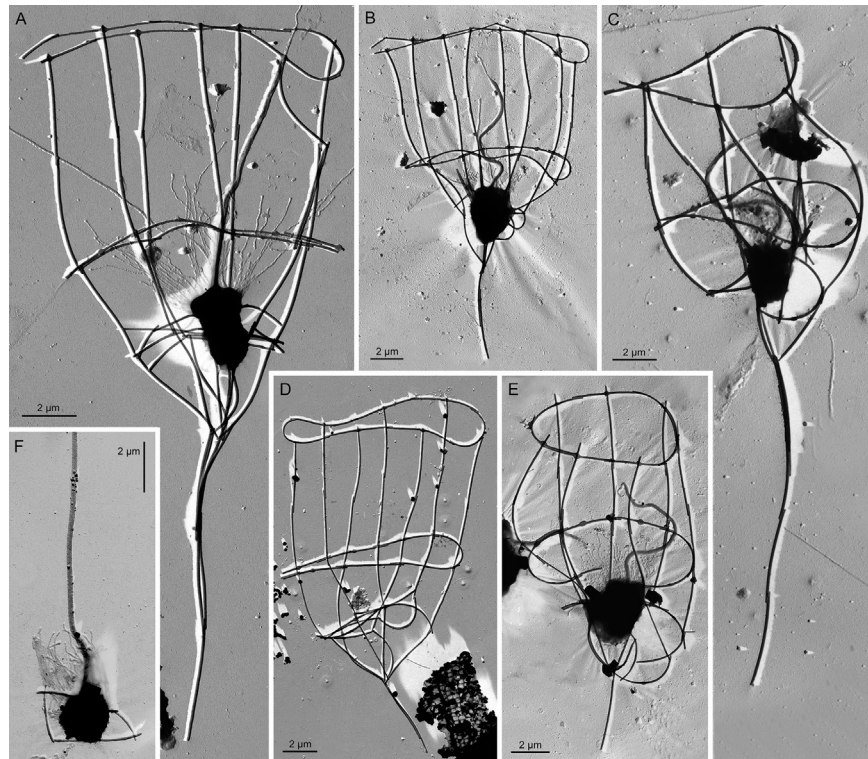


Fig. 16. TEM whole mounts from Disko Bay of *Polyfibula caudata* (A-D) and *Monocosta fennica* (F). Notice (A-E) variations in the number of longitudinal costae and the occurrence of small anterior projections in one lorica (E). The *M. fennica* lorica comprises approx. 5 costal strips organized in a single transverse costa.

costal strips) and 3 transverse costae, i.e. a costa that closes the lorica anteriorly ('E'-joins), and transverse costae at the level of the junctions between the second/third and third/fourth longitudinal costal strips. Variations on this theme include in addition to the number of longitudinal costae, the overall lorica size, minor shifts with reference to the actual positioning of the second transverse costa), the relative sizes of the anterior transverse costae, and the occasional presence of anterior or posterior spines. The genus and its associated species were described based on material from the Indian Ocean (Thomsen and Boonruang, 1984), although a specimen from Denmark was selected as the generic type (*C. norvegica*).

Two species of *Cosmoeca* are among the community dominants in Greenland waters (Fig. 2), i.e. *C. norvegica* (see e.g. Thomsen, 1982; loc. cit. Fig. 73; referred to as choanoflagellate sp. 'N') and *C. ventricosa* (Fig. 14). Also found are specimens of *C. takahashii* (Fig. 14G-H), a species which was for a period considered endemic to Antarctic waters. The recording (Table 1) of *C. phuketensis* from Igloolik (Arctic Canada) is perhaps erroneous and it is likely, considering the findings reported below, that the identity of this material is rather *C. ventricosa* form C.

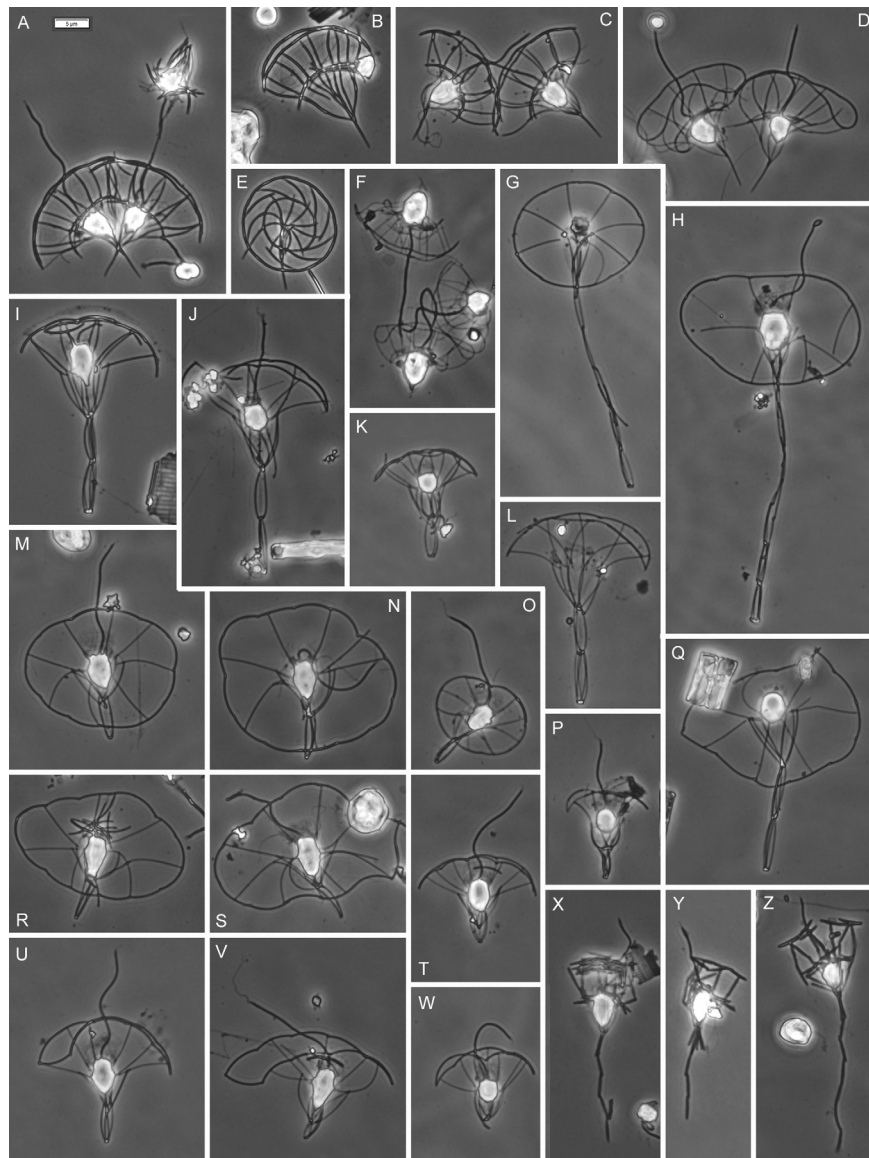


Fig. 17. *Parvicorbicula* spp. **A-F:** *Parvicorbicula socialis* from NEW (A, C-F) and NOW (B); the cells illustrated display pronounced size and costal strip thickness variability; one cell (A) is undergoing division. **G-W:** *Parvicorbicula manubriata* from Disko Bay (I-J) and NEW (G-H, K-W); the cells selected primarily show the morphological variability encountered in the NEW tank experiment (K-X), but also the long stalked specimens (G-H) that are sometimes found in ice biota samples. **X-Z:** *Parvicorbicula serrulata* from NEW (X, Z) and NOW (Y). The scale bar (A) applies to all LM images.

It has since long been recognized that the variability encountered within the *C. ventricosa* complex goes beyond what was originally accounted for by [Thomsen and Boonruang, 1984](#); (*C. ventricosa* and *C. ventricosa* form A-C), and further that regional variability may differ from place to place, e.g. necessitating the addition of a *C. ventricosa* form D (cells with a pedicel formed by one costal strip) based on material from the Weddell Sea ([Thomsen et al., 1990](#)). To advance our

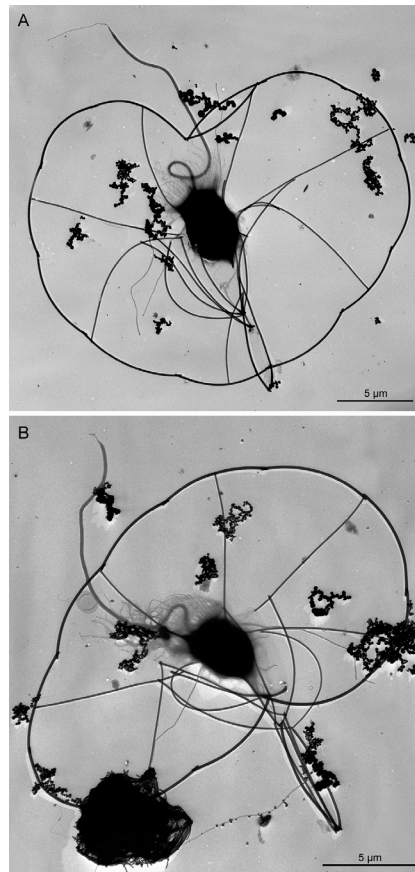


Fig. 18. *Parvicorbicula manubriata* TEM specimens from the NEW tank experiments. Notice in both specimens the irregularities in patterns of attachments between longitudinal and anterior transverse costal strips (mostly irregular T-joins and the occasional E-join).

understanding of the *C. ventricosa* variability matrix and assemble an overview of the variability encountered in habitats that are vastly different from those examined by Thomsen and Boonruang (1984), we have here undertaken a thorough analysis of the communities encountered in Greenland waters based on light microscopy (Figs. 14 –15 ; Table 4).

The smallest specimens encountered (Fig. 14 R-W; lorica height 12–14 µm and anterior diam. 9–11 µm) have predominantly 10 longitudinal costae (ca. 75% of all loricae examined; see Table 4) and a middle transverse costa that is significantly smaller than the anterior transverse costa. These forms are thus very similar to *C. ventricosa* form C as described from the Indian Ocean. It is evident from Fig. 15A, which summarizes findings from the NEW and NOW polynya and from Disko Bay, that these organisms (*C. ventricosa* form C) are very conservative regarding lorica dimensions.

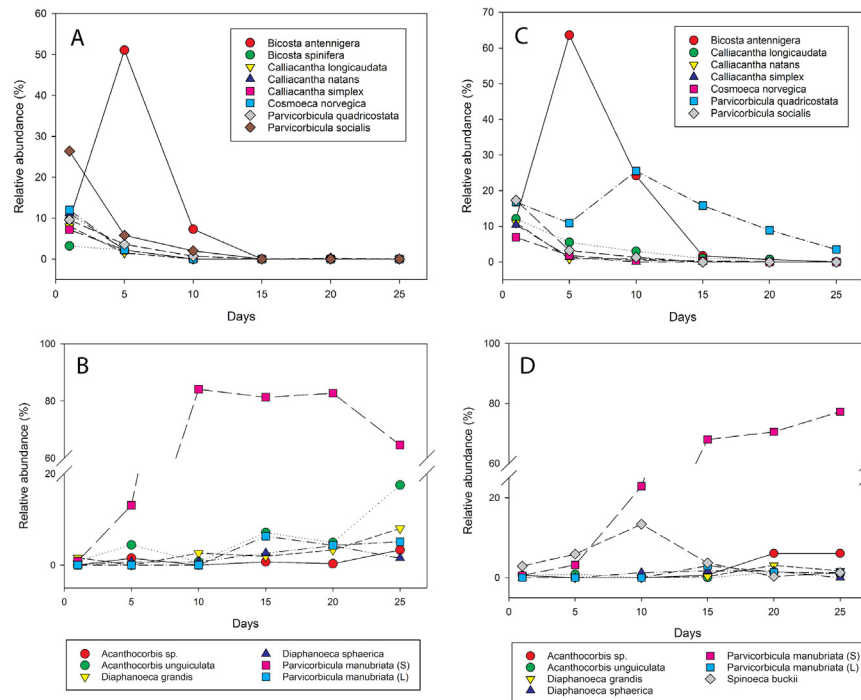


Fig. 19. Loricate choanoflagellate community development during NEW tank experiments. Experiment 1 (A, B); experiment 2 (C, D). Species with decreasing relative abundance are shown in panels A, C, and those with increasing relative abundance in panels B, D.

A second group of small specimens of *C. ventricosa* related forms (Fig. 14L, X–Ac) consistently have 12 longitudinal costae (Table 4) and a middle transverse costa that is only marginally smaller than the anterior transverse costa (Fig. 15A–B). The lorica height is 11–14 μm and the anterior transverse costa diameter

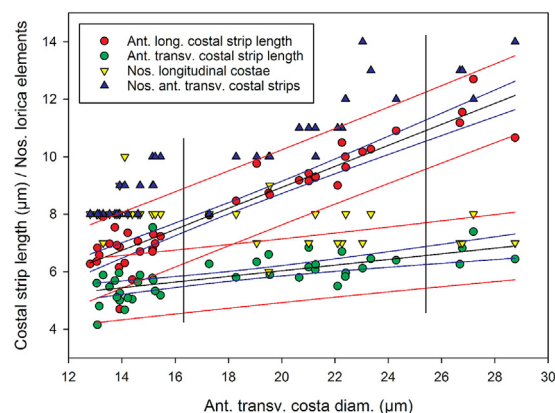


Fig. 20. Morphometric characteristics of the *Parvicorbicula manubriata* specimens from the NEW tank experiments. See text for further explanations. Linear regressions show how costal strip length varies when the anterior transverse costa increases in size. Also shown are the 95% confidence and prediction bands. The vertical lines separate three size groups of specimens.

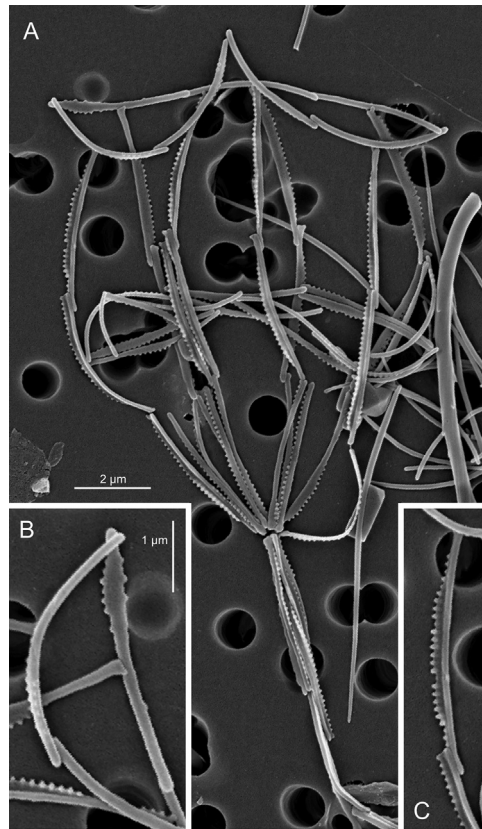


Fig. 21. *Parvicorbicula serrulata* SEM images from Svalbard (courtesy of Mikal Heldal). (A) whole cell; (B) Detail of anterior transverse costa; (C) Detail of longitudinal costa.

ranges between 9–13 μm . This is a well-defined sub group of *C. ventricosa* forms not previously recognized and they should accordingly in the future be referred to as *C. ventricosa* form E.

There is a third group of slightly larger *C. ventricosa* specimens that has proved to be very stable in terms of lorica dimensions and numerical details across the geographic areas sampled here (Table 4). These forms (Fig. 14A–F; see also Thomsen, 1982; loc. cit. Figs. 81–85) have nine longitudinal costae (96% of all loricae examined; see Table 4) and a middle transverse costa that is only marginally smaller than the anterior transverse costa. The overall lorica height varies between 17 and 22 μm and the anterior transverse costa diameter between 11–16 μm . It is evident from Fig. 15 A that these small-sized forms with 9 longitudinal costae cluster densely. The *C. ventricosa* form A described from the Indian Ocean (Thomsen and Boonruang, 1984) has 10 longitudinal costae but is otherwise very similar to those illustrated here. It therefore appears acceptable to also refer to the Greenland specimens as form A.

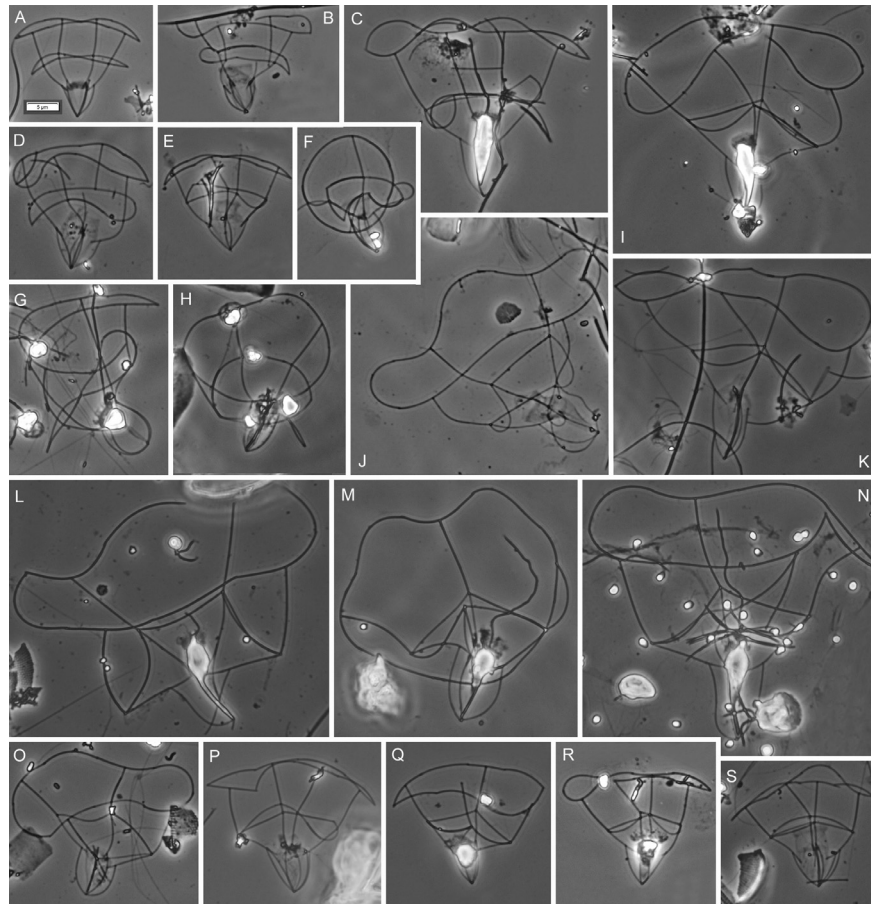


Fig. 22. *Parvicorbicula* spp. A-H: *Parvicorbicula circularis* from Disko Bay (A-F), NEW (G), and NOW (H). I-S: *Parvicorbicula quadricostata* from Disko Bay (I-K, O, Q), NEW (M-N, P, S), and NOW (L, R). The bright dots (N) are *Micromonas pusilla* specimens. The scale bar (A) applies to all LM images.

Whereas the smaller sized forms of *C. ventricosa* show little variability in lorica dimensions and the number of longitudinal costae, the overall variability is much more pronounced when examining larger sized forms of this species (Fig. 14 I-K, M-Q and Table 4). These loricae that range in height from 24–43 μm and in anterior transverse costa diameter from 15–32 μm , may comprise 9–12 longitudinal costae (Fig. 15 A). There is an interesting tendency towards a reduction in the number of longitudinal costae when lorica sizes are increasing (Fig. 15A). There are obvious mechanical differences among the larger sized loricae regarding structural stability. Whereas the smaller versions (e.g. Fig. 14O–P) appear to be fairly robust, the larger forms (e.g. Fig. 14K, M) tend to be more irregularly flaring and with a tendency of collapsing when dried down in a much less controlled and consistent way. There are at this stage no immediate morphometric or morphological handles that can be used to convincingly separate out additional *C. ventricosa* forms among the larger sized specimens.

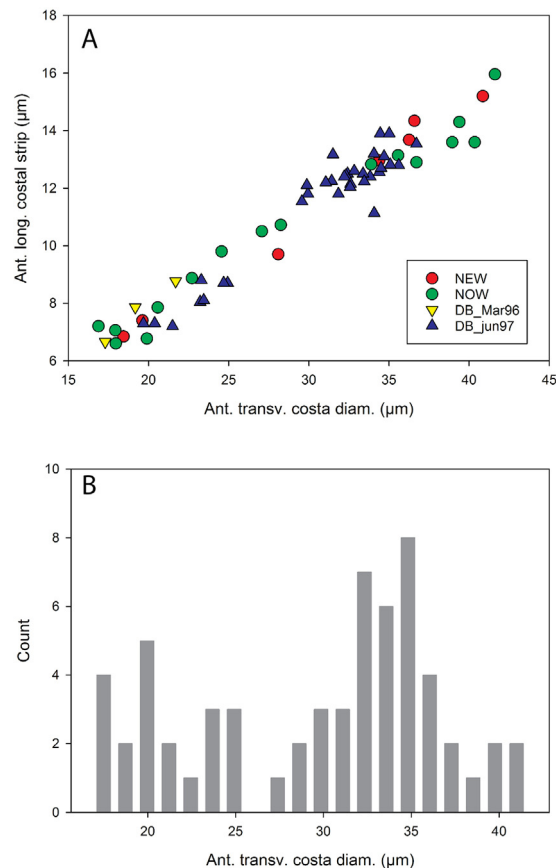


Fig. 23. *Parvicorbicula quadricostata* size variability across the regions sampled. There is a linear relationship in dimensions when comparing small and large specimens (A), and a trend towards a bimodal distribution of the specimens analyzed (B).

The *C. ventricosa* lorica is generally characterized by equally sized anterior and middle transverse costa diameters (Fig. 15B). However, the best fit to the entire data set is a non-linear regression ($R = 0.9614$; $R_{\text{sqr}} = 0.9243$). In small and large loricae there is a tendency towards a decrease in costa diameter when moving from the anterior to the middle transverse costa. In medium-sized loricae the middle transverse costa is usually equal to or slightly larger than the anterior transverse costa. Whereas Fig. 15A is a composite diagram that displays information on all specimens analysed, the contributions and characteristics of each of the three major sites sampled appear from Fig. 15C–E.

As presently circumscribed the species *C. ventricosa* thus comprises a main form (i.e. specimens with larger sized loricae and 9–12 longitudinal costae) and five forms (A–E). Form B (not mentioned above) is characterized by anteriorly projecting short spines (Thomsen and Boonruang, 1984). Molecular tools will be needed to more decisively determine a proper way to deal with the encountered variability within the *C. ventricosa* complex. It will most likely be relevant to

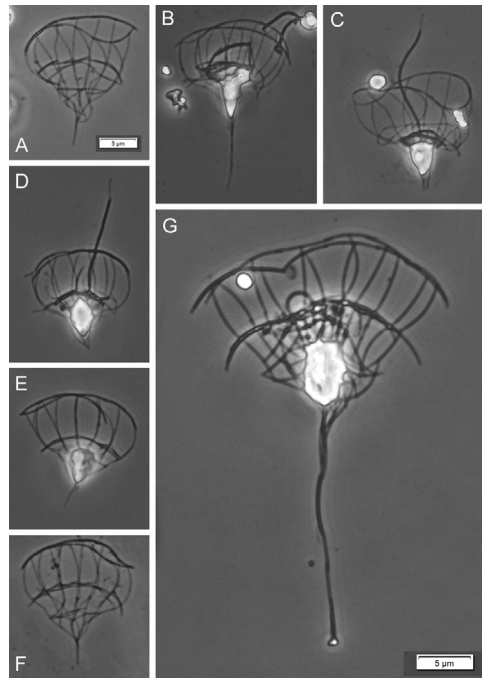


Fig. 24. *Parvicorbicula* spp. **A-F:** *Parvicorbicula* cfr. from NOW (**A-C**) and NEW (**D-F**). **G:** *Parvicorbicula pedunculata* from NEW. The scale bar (**A**) also applies to **B-F**.

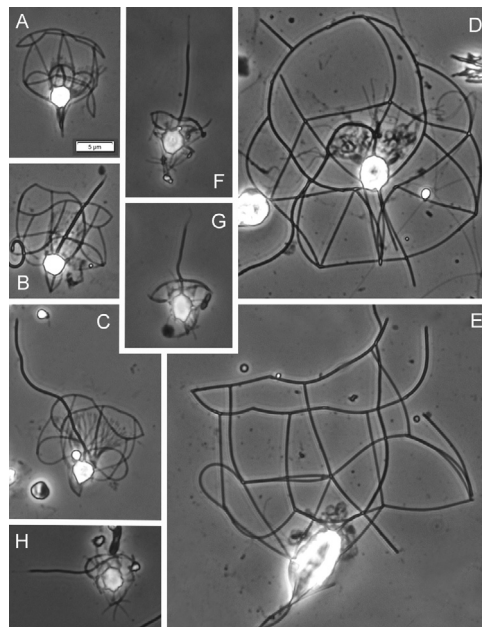


Fig. 25. *Pleurasiga* spp. (**A-E**), and *Nannoeca minuta* (**F-H**). **A-C:** *Pleurasiga minima* from NOW. **D-E:** *Pleurasiga reynoldsii* from NOW. **F-H:** *Nannoeca minuta* from Disko Bay. The scale bar (**A**) applies to all LM images.

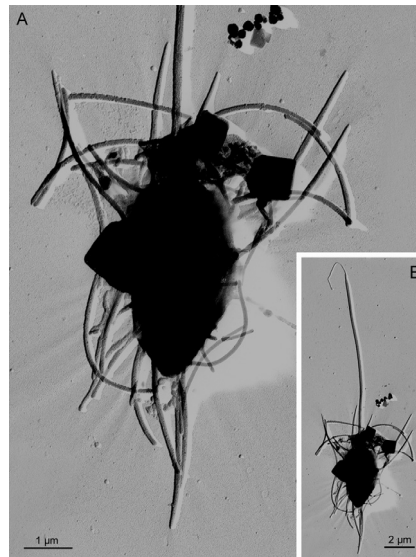


Fig. 26. *Nannoeca minuta* TEM micrograph showing a Disko Bay 1990 specimen. (A) Loric chamber with very conspicuous anterior spines; (B) Complete cell.

describe some of the forms (e.g. *C. ventricosa* form C and E) as separate taxa, whereas it appears more likely that *C. ventricosa* form A may represent the small sized lorica version in a bimodal size spectrum of the main form of *C. ventricosa*. An alternative approach while awaiting molecular supportive taxonomic evidence is to continue recording the variability encountered within geographically well-defined regions according to the principles and tools (LM) applied here. This will eventually lead to the assembly of a robust morphometric matrix that can in turn become the basis for a split-up in multiple species.

3.5.2.3.2. Polyfibula

Manton 1981 in Manton and Bremer, 1981 (Fig. 16). The genus *Polyfibula* comprises species characterized by small and fairly simple obconical loricae comprising 6–9 longitudinal costae and 3 transverse costae. The transverse costae occur at the anterior opening of the lorica and at the joins between the second and third versus the third and fourth longitudinal costal strip respectively (Fig. 16 A). There are T-joints anteriorly, and the longitudinal costae attach here to facets placed in the middle of each transverse costal strip. Facets also occur in the middle transverse costa where the longitudinal costae attach to the joins between neighbouring costal strips.

The genus currently comprises five taxa, i.e. *P. sphyrelata* (Thomsen, 1973) Manton in Manton and Bremer, 1981; *P. caudata* (Leadbeater in Manton et al., 1975) Manton in Manton and Bremer, 1981; *P. elatensis* (Thomsen, 1978) Manton in Manton and Bremer, 1981; *P. hexacostata* Manton in Manton and Bremer,

Table 4. Lorica dimensions (μm) of specimens from the *C. ventricosa* complex. Measurements from dried material which causes a certain reduction in size of organic components. Lorica diameters are calculated based on measurements of the lorica circumferences.

	Material	Flagellum	Protoplast length	Range	Protoplast width	Range	Lorica height	Range	Diam. ant. transverse costa	Range	Diam. middle transverse costa	Range	Diam. post. transverse costa	Range	Longitudinal costae (number)	n (max.)			
																9	10	11	12
<i>C. ventricosa</i> A	NEW	22.3 \pm 6.1	5.0 \pm 1.1	3.9–6.8	3.6 \pm 0.4	2.9–4.2	19.3 \pm 1.2	18.1–22.4	13.8 \pm 0.9	12.8–15.6	11.4 \pm 0.9	10.4–13.5	4.6 \pm 0.5	4.2–4.9	10	1			11
	NOW	21.8 \pm 4.4	6.0 \pm 0.7	4.6–7.4	3.9 \pm 0.4	3.1–4.9	19.2 \pm 1.1	17.7–21.4	13.7 \pm 0.9	11.4–14.9	11.7 \pm 0.7	10.4–13.0	4.7 \pm 0.6	3.9–5.8	23	1			24
	Disko Bay	12.6	4.6 \pm 0.8	3.5–6.1	3.3 \pm 0.3	2.9–3.9	19.8 \pm 1.6	16.8–22.1	13.5 \pm 1.1	11.6–15.9	11.4 \pm 0.8	9.8–12.3	5.4 \pm 0.3	5.0–5.8	10				10
<i>C. ventricosa</i> C	NEW	13.9	3.5 \pm 0.2	3.3–3.7	2.8 \pm 0.3	2.6–3.1	13.6 \pm 0.5	13.1–14.2	10.2 \pm 0.5	9.4–10.7	6.8 \pm 0.4	6.3–7.2	4.0 \pm 0.6	3.6–4.4	1	3			4
	NOW	13.9	3.5 \pm 0.5	2.9–4.3	2.7 \pm 0.4	2.5–3.4	13.6 \pm 0.8	12.2–14.2	10.4 \pm 0.5	9.8–11.2	6.9 \pm 0.6	6.1–7.7	4.5		5	1	1		7
	Disko Bay		3.9			2.7	13.9 \pm 0.3	13.5–14.2	9.8 \pm 0.4	9.5–10.3	6.7 \pm 0.6	6.1–7.5	3.5 \pm 0.5	3.0–3.9	3	1			4
<i>C. ventricosa</i> E	NEW	15.0 \pm 3.0	3.4 \pm 0.7	2.3–4.2	2.5 \pm 0.3	2.1–2.9	12.5 \pm 1.0	10.8–13.5	10.5 \pm 0.9	8.8–11.3	8.6 \pm 0.7	8.0–9.7						6	6
	NOW	14.8 \pm 2.9	3.4 \pm 0.5	2.6–4.3	2.7 \pm 0.3	2.2–3.4	12.5 \pm 0.8	11.2–13.6	10.6 \pm 0.7	9.0–11.7	8.4 \pm 0.6	7.8–10.0						13	13
	Disko Bay						11.4 \pm 0.8	10.8–11.9	11.8 \pm 1.5	10.8–12.9	7.9 \pm 0.5	7.5–8.3						2	2

(Continued)

Table 4. (Continued)

	Material	Flagellum	Protoplast length	Range	Protoplast width	Range	Lorica height	Range	Diam. ant. transverse costa	Range	Diam. middle transverse costa	Range	Diam. post. transverse costa	Range	Longitudinal costae (num- ber)	n (max.)
C. ventri- cosa	NEW		6.5 ± 1.6	5.2–8.2	4.7 ± 0.6	4.2–5.3	31.1 ± 3.0	27.9–35.2	23.3 ± 0.7	22.7–24.2	22.6 ± 2.1	20.4–25.1	6.9		4	4
	NOW	21.3 ± 5.4	7.4 ± 1.2	6.3–9.7	4.3 ± 0.9	2.6–5.6	27.7 ± 2.8	24.0–32.2	19.7 ± 3.4	14.5–24.3	18.6 ± 3.5	13.5–24.2	6.2 ± 1.4	4.5–8.1	13	13
	Disko Bay	41.3	5.9 ± 3.3	3.3–9.7	4.1 ± 1.3	3.0–5.6	29.3 ± 0.8	28.3–29.8	20.4 ± 2.2	17.5–23.0	20.50.9	19.3–21.8	8.1 ± 1.4	6.6–9.3	3 4 1	8
	Disko Bay ¹	17.4 ± 3.5	8.7 ± 1.4	6.3–10.4	4.0 ± 0.4	3.5–4.6	36.2 ± 4.0	31.0–42.8	28.7 ± 2.6	24.8–31.9	26.3 ± 1.9	24.1–29.3			7	7

¹Material from June 1997.

Table 5. Distinguishing characters among species of *Polyfibula* (based on [Manton and Bremer 1981](#)). Additions to the original Table (with reference to the number of longitudinal costae) are indicated in bold face. The * identifies the main diagnostic feature for each species (except for the generic type).

Taxon	Long. costae (number)	Projections Posterior	Projections Anterior	Distribution	Comment
<i>P. sphyrelata</i> (generic type species)	7–8– 9 -		0-slight	Denmark (Thomsen, 1973), New Zealand (Moestrup, 1979), S. Africa (Manton and Bremer, 1981)	Specimens with 9 longitudinal costae are found in Danish waters (Thomsen, unpublished)
<i>P. caudata</i> (syn. <i>P. stipitata</i>)	6– 7 3 strips*		0	Hudson Bay (Manton and Bremer, 1981); Disko Bay (this paper)	This paper Fig. 16A (7 long. costae)
<i>P. elatensis</i>	7– 8 – 9 1–2 strips		Long (=½ strip)*	Red Sea (Thomsen, 1978), Galapagos Islands and North Alaska (Manton and Bremer, 1981), Denmark (Thomsen, unpublished)	8 long. costae (Manton and Bremer, 1981)/9 long. costae found in Danish material (Thomsen, unpublished)
<i>P. stipitata</i> (<i>P. caudata</i> syn.)	7– 8 1–2 strips		0-slight	Arctic Canada, North and South Alaska (Manton and Bremer, 1981)	This paper (Fig. 16B) (8 long. costae)
<i>P. hexacostata</i>	6* -		0-slight	South Alaska (Manton and Bremer, 1981)	

1981; and *P. stipitata* Manton in Manton and Bremer, 1981. The distinguishing characters are summarized in Table 5.

Tong, (1997a) concluded following a survey of *Polyfibula* spp. from Southampton Water (UK) that it seemed difficult to justify the separation of the genus into 5 species and therefore suggested that *P. caudata*, *P. stipitata* and *P. hexacostata* were all reabsorbed into *P. sphyrelata*. Manton and Bremer (1981) based their species matrix on the number of longitudinal costae and the presence or absence of anterior and posterior projections. Characters such as the number of longitudinal costae and the extent of a posterior projection are, however, known to be variable across a major sub-set of all loricate choanoflagellate species. After an update of Table 5 (based on Manton and Bremer, 1981; loc. cit. Table 2) with new information it now seems even less appropriate to apply the number of longitudinal costae as a feature that efficiently distinguishes species. We recommend accordingly, while taking a slightly less radical approach as suggested by Tong, (1997a) that *P. stipitata* is relegated to a synonym of *P. caudata* which is henceforth now defined by having 6–8 longitudinal costae, a posterior projection that is variable in length (1–3 costal strips), and 0-slight projections anteriorly (Fig. 16A–E). The *P. caudata/stipitata* complex is thus distinguished from the type species, *P. sphyrelata*, by the presence of a posterior projection. *Polyfibula elatensis* remains a well-defined taxon due to the presence in this species of very long anterior projections. For the time being we recommend that *P. hexacostata* is maintained as a separate taxon. The material examined by Manton and Bremer, (1981) from South Alaska shows a species that is easily distinguished from other forms of *Polyfibula* based on both morphometric and morphological causes, i.e. 6 long. costae, small lorica size, no posterior projections and consistently thickened costal strips.

While specimens of *Polyfibula* are frequently occurring in West Greenland samples (Table 1) we have not found *Polyfibula* spp. in any of the high arctic samples analyzed here.

3.5.2.3.3. Monocosta

Thomsen, 1979 (Fig. 16) This monotypic genus (*M. fennica*; Fig. 16F) was first described from the innermost part of the Baltic Sea (Thomsen, 1979) and has later been sparingly observed again in Baltic Sea samples (Vørs, 1992; Ikävalko and Thomsen, 1997; Ikävalko, 1998). The lorica is extremely reduced and comprises only a single transverse costa made from five costal strips. The relationship of this genus to other acanthoecid genera is unclear in as much as the *M. fennica* lorica resembles the posterior transverse costa in a number of genera, e.g. *Polyfibula*. A single specimen (Fig. 16F) was observed in a sample from Disko Bay 1990 at a depth of 100 meter.

3.5.2.3.4. Parvicorbicula

Deflandre, 1960 (Figs. 17–24) The genus *Parvicorbicula* is represented in the high Arctic by five species, i.e. *P. circularis*, *P. manubriata*, *P. quadricostata*, *P. serrulata* and *P. socialis*, and more of these frequently occur as community dominants (Fig. 2). Two additional species (*P. pedunculata* and *P. superpositus*) are included in Table 1. The latter species has been described from the subarctic North Pacific Ocean (Booth, 1990), however, it still has its main distribution at lower latitudes. The finding of *P. pedunculata* from Igloolik (Canadian Arctic) is not accompanied by illustrations from either LM or TEM (Daugbjerg et al., 1991) and must hence be accepted with an element of uncertainty, although the finding of this species also from the Gulf of St. Lawrence (Bérard-Therriault et al., 1999) and from the NEW polynya (as *P. pedunculata* cfr.; see further below) renders the observation more plausible.

Parvicorbicula socialis (Fig. 17A–F) has the capacity to form large colonies where neighbouring cells attach along the anterior transverse costa. This characteristic explains that this species was described more than 100 years ago, from the Kara Sea (Meunier, 1910; as *Corbicula socialis*) and also why it has been frequently reported in the context of general protist plankton surveys based on net tows or the examination of sedimented samples (e.g. Braarud, 1935). Pairwise linkage of cells is shown in e.g. Fig. 17C–D. *Parvicorbicula socialis* has a very consistent appearance in terms of structural lorica features. There are constantly 10 longitudinal costae that amalgamate and adjoin posteriorly to be continued into a short pedicel, and two transverse costae. The anterior transverse costa surmounts the longitudinal costae and attaches to these by means of T-joints. The posterior transverse costa is smaller and displaced by one longitudinal costal strip. Manton et al. (1976) when examining Arctic material of *P. socialis* pointed to the existence of two morphotypes within this species, an observation that has been found to be generic when dealing with this taxon. While the two forms, Fig. 17A–B, E and Fig. 17C–D, F respectively, share the structural details accounted for above, they differ in size by approximately 20 percent and costal strip robustness. Manton et al. (1976) were inclined, since only one type of lorica seemed at a given time to represent living material as verified from the presence of a protoplast, to interpret these morphological shifts as indicative of seasonality within the population. Our findings from the NEW and NOW polynya and Disko Bay most often comprise mixtures of the two forms with intact cells co-occurring, yet often shifted with a community dominance of one form or the other. Seasonality or rather environmental impact of one kind or the other is still a likely explanation, although it may also be relevant on top of this to consider the possibility that the phase shifts are somehow linked to an as yet unresolved life cycle expression (Thomsen and Østergaard, 2017). *Parvicorbicula socialis* has a worldwide distribution yet with a preference for high latitude colder waters (Fig. 3).

Parvicorbicula manubriata was first described from Southampton waters (Tong, 1997a) and was later further illustrated and analysed based on material from the Danish Wadden Sea and the NEW polynya ice biota (Thomsen et al., 1997). There is in this species (Fig. 17I, L and Fig. 18A–B) a single anterior transverse costa which surmounts the longitudinal costae that each comprise two costal strips. The posteriorly free tips of the anterior tier of longitudinal costal strips attach to the membrane that wreathes the protoplast (Fig. 18B). A handle-like stalk comprising a cluster of costal strips arranged in parallel and with the bended tips pointing inwards (Fig. 18B) is a conspicuous lorica feature in this species. There is typically 1–2 of these ‘handles’ but occasionally there may be as many as 6 tiers (Fig. 17G–H). A unique feature of this species is the irregularities observed in the number of longitudinal costae and the number of anterior transverse costal strips which frequently departs from a 1:1 ratio resulting in fortuitous patterns of contact between transverse and longitudinal costal elements. This is best seen in Fig. 18A–B but also visible in the light micrographs, e.g. Fig. 17M–N.

Access to a rich material of *P. manubriata* specimens from the NEW polynya has permitted us to further examine the principles behind the observed variability in *P. manubriata* morphometrics. The material originates from mesocosm experiments carried out on board the RV ‘Polarstern’ (Bauerfeind et al., 1994). During a 30-day period each of the 1000 litre tanks were sampled with 5-days intervals and screened for the occurrence of loricate choanoflagellates (Fig. 19A–B, C–D). The upper panels (Fig. 19A, C) show relative abundances for taxa that basically vanished during the time span of the experiment. The conspicuous peak of *Bicosta antennigera* on day 5 in both tanks is noteworthy, as is also a more delayed peak in

Table 6. *Parvicorbicula manubriata* size variability (NEW tank experiment). The size classes are visually depicted in Fig. 20.

Lorica element	Size groups	Mean	St.dev.	Max.	Min.	n
Ant. transv. costa diam.	Small	14.1	0.81	15.5	12.8	21
	Medium	21.1	1.88	24.3	17.3	17
	Large	27.4	0.96	28.8	26.7	4
Ant. long. costal strip length	Small	6.7	0.68	7.9	4.7	21
	Medium	9.4	0.77	10.9	8	17
	Large	11.5	0.87	12.7	10.7	4
Ant. transv. costal strip length	Small	5.4	0.68	7.5	4.2	20
	Medium	6.2	0.36	6.8	5.5	17
	Large	6.7	0.5	7.4	6.3	4

relative abundance of *Parvicorbicula quadricostata* in one of the tanks (Fig. 19C). The overall picture is generally that of a decline in relative abundance of the open ocean pelagic forms. The lower panels (Fig. 19B, D) show the development over time in relative abundance of loricate choanoflagellate species that gained from the entrapment of sea water leading to a much-altered physical environment characterized by less turbulence and the introduction of a vastly increased surface areas. The species benefitting from this change of scenery are those that are either associated with near coastal habitats (*Diaphanoeca grandis*, *Acanthocorbis unguiculata*) or prevalent within sea ice (*Acanthocorbis* sp., *Parvicorbicula manubriata*). As is evident from Fig. 19B, D small specimens of *Parvicorbicula manubriata* (e.g. Fig. 17O, T) completely dominated both tanks from day 10 and reached a relative abundance of 80% towards the end of the experiments. The larger sized morphotype of *P. manubriata* (e.g. Fig. 17M–N, R–S) peaked around day 15 in both experiments (Fig. 19 B, D) but never reached abundances exceeding 5%. The size variability among lorica elements and numerical characteristics across a large selection of specimens is accounted for in Table 6 and Fig. 20. It appears from Fig. 20 that it is possible to distinguish between three size fractions (small-medium-large cfr. Table 6) when scrutinizing the entire material. The small cells have almost exclusively 8 longitudinal costae (rarely 7 or 10), and mostly 8 but also occasionally 9 or 10 transverse costal strips in the anterior ring. Middle sized cells have 7–8 (rarely 6) longitudinal costae and 10–11 (occasionally up to 14) transverse costal strips. The large specimens are characterized by 7–8 longitudinal costae and 12–14 anterior transverse costal strips. Considering the variability in numbers accounted for above it is obvious that patterns of interconnections between transverse and longitudinal costal elements have to be highly variable.

The twofold increase in size (from roughly 14 to 28 μm when considering the diameter of the anterior transverse costa) is with respect to the longitudinal costae accomplished through a corresponding doubling (Fig. 20) in costal strip length (from 6.7 to 11.5 μm /Table 6). The increase in size of the anterior transverse costa is only to a small extent (<25%; see Table 6) accounted for through an elongation of the individual costal strip (Fig. 20) but rather accomplished through an increase in the number of strips utilized (from 8 to 14).

The size variability accounted for here and the principles behind (extension in length of longitudinal strips and a simultaneous increase in number of transverse strips) are so significant and complex that it likely goes beyond what can be referred to as chance like variability. The delayed appearance of large specimens (day 15) also points to that something has triggered the *P. manubriata* specimens to not exclusively repeat during division a similar design to that of the parental cell. For the time being we have no specific explanation at hand and we will rather suggest that the scenario presented here is added to the list of unorthodox division

patterns encountered among loricate choanoflagellates (Thomsen and Østergaard, 2017).

Parvicorbicula serrulata was originally described (Manton et al., 1975) from Resolute Bay, Cornwallis Island (Arctic Canada). It has since then been found at all arctic sites sampled and reported here (Table 1) and it is also known from Svalbard (Mikal Heldal, unpublished). *Parvicorbicula serrulata* is easily recognized from LM (Fig. 17X–Z) because of the broad costal strips, the long pedicel and cluster of strips that typically diverges from the hind end of the lorica. A SEM image of a *P. serrulata* specimen from Svalbard is reproduced here as Fig. 21. It shows some variability in costal strip ornamentation when compared with the type material. Both the transverse and longitudinal costal strips have thus fewer and on the longitudinal costal strips apparently unilateral indentations. All costal strips are asymmetrical along major axes. It is evident from the SEM image that the longitudinal costae are exteriorly located compared to the posterior transverse costa. *Parvicorbicula serrulata* has not so far been observed outside the Arctic realms and remains the only cold water species with exclusively flattened costal strips.

Parvicorbicula circularis (Fig. 22A–H) is observed at all major sites analysed here. This species was first described from Danish coastal waters (Thomsen, 1976) but has later been found to have a cosmopolitan distribution (Fig. 3). The distinguishing feature for this taxon, in comparison with *P. quadricostata* is the appearance of the posterior transverse costa, which is square in the latter, while circular and formed by 6–8 costal strips in the former. The Arctic material exclusively comprises forms with 6 costal strips. Most of the specimens are small (Fig. 22 A–B, D–F; ant. transverse costa diam. ca. 15 µm), however, the occasional

Table 7. *Parvicorbicula quadricostata* size variability in Greenlandic waters.

Lorica element	Size group	Mean	St. dev.	Min.	Max.	n
Ant. transv. costa diam.	Small	20.9	2.57	16.9	24.9	20
	Large	34.0	3.33	27.1	41.6	41
Lorica height	Small	20.9	2.82	15.4	27.4	19
	Large	33.6	3.54	26.7	42.8	39
Ant. long. costal strip	Small	7.8	0.90	6.6	9.8	20
	Large	12.7	1.17	9.7	16	41
Post. transv. costal strip	Small	8.5	1.03	6.8	10.5	20
	Large	13.6	1.30	10.7	16.2	41

larger sized individuals (Fig. 22C, G–H; ant. transverse costa diam. ca. 25 μm) do also occur. A similar bimodal lorica size distribution was previously documented from Antarctic waters (Thomsen et al., 1990). The organic sheath that encapsulates the protoplast is very evident also in LM images of *P. circularis* (see e.g. Fig. 22B, D–F).

Parvicorbicula quadricostata was first light microscopically described from Bear Island (Barents Sea) by Throndsen (1970b) and has later been frequently reported from in particular high latitude habitats (Fig. 3). A thorough re-examination of the species including TEM observations was provided by Manton et al. (1976). The evidence for a bimodal size distribution is convincing in the case of *P. quadricostata*. Small specimens (Fig. 22 O–S; transverse costa diam. 21 μm /lorica height 21 μm) occur at all sites sampled except for the Disko Bay material from March 1996 (Fig. 23A) together with larger sized specimens (Fig. 22 I–N; transverse costa diam. 34 μm /lorica height 34 μm) (Table 7; Fig. 23A). The bimodal size distribution is further visualized in Fig. 23B. The material from Disko Bay June 1997 unambiguously shows the two-peaked size distribution (Fig. 23A), whereas the polynya material does have a non-uniform distribution, yet also comprises forms that size-wise link the extremes. The type description of *P. quadricostata* (Throndsen, 1970b) states that the maximum diameter at the level of the anterior transverse costa is 24 μm which places this material within the small-sized category.

Parvicorbicula pedunculata was first described from South Brittany, France, by Leadbeater (1980). It has later been reported from the Gulf of St. Lawrence by Bérard-Therriault et al. (1999) where the findings are convincingly documented by SEM and LM micrographs, and from Igloolik (Arctic Canada) by Daugbjerg et al. (1991) without accompanying illustrations. The single cell (Fig. 24G) found in the NEW mesocosm experiment organized by Bauerfeind et al. (1994), is reminiscent of *P. pedunculata* yet significantly larger (overall length: 40 μm , lorica chamber height: 19 μm , ant. transv. costa diam.: 19 μm as opposed to 20–26 μm , 13–14 μm and 8–12 μm respectively in the type material) and with 12 rather than 9–10 longitudinal costae (Leadbeater, 1980). The St. Lawrence material (Bérard-Therriault 1999) is on the other hand almost identical to the French type material when considering specifically the variant described with 10 longitudinal costae (Leadbeater, 1980).

Whenever examining a large quantity of loricate choanoflagellates, there is always a small contingent of cells that cannot easily be identified or even loosely referred to a specific taxon. Such cells with resemblances pointing in the direction of both *Cosmoeca* and *Parvicorbicula* (*P. socialis* cfr.) are illustrated in Fig. 24A–F. It is not possible without access to TEM micrographs of these forms to unravel their

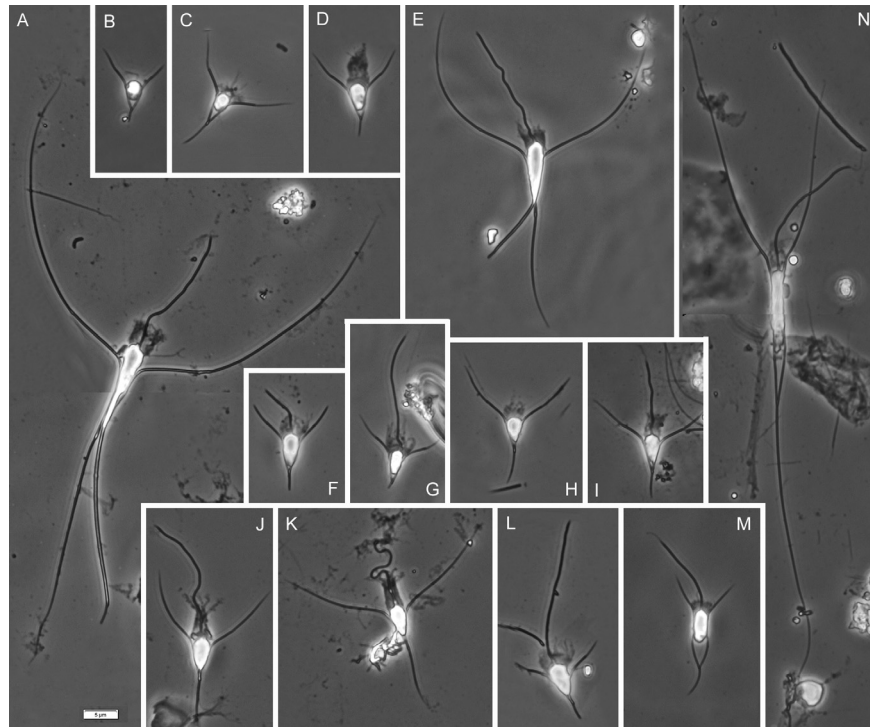


Fig. 27. *Bicosta* spp. **A-L:** *Bicosta antennigera* from NOW (A-C, G, I-K), NEW (D-F, L), and Disko Bay (H) showing an extreme variability in overall lorica size. The specimens (A, E) are in the process of preparing for cell division. **M:** *Bicosta minor* from NEW. **N:** *Bicosta spinifera* from NOW. The scale bar (A) applies to all LM images.

possible identities, however, for the sake of completeness it is considered relevant to include these forms here.

3.5.2.3.5. Pleurasiga

Schiller 1925 (Fig. 25) This genus is represented in Arctic waters by only two species, i.e. *P. minima* (Fig. 25A–C) and *P. reynoldsii* (Fig. 25D–E) which often occur as community dominants (Fig. 2). Both species were described from the Barents Sea (Bear Island) by Thronsdén (1970b) and have later been found to be widely distributed (see e.g. Fig. 3/*P. minima*). The diagnostic features as outlined by Thronsdén (1970b) and later confirmed by Manton et al. (1976) allows for an easy LM identification of these taxa which appear to be very stable across their distributional ranges with respect to both numerical details as well as overall dimensions.

3.5.2.3.6. Nannoeca

Thomsen, 1988 (Figs. 25–26) This monotypic genus (*N. minuta*; Fig. 25 F–H and Fig. 26A–B) is widely distributed globally (Fig. 3) yet sparsely recorded from high

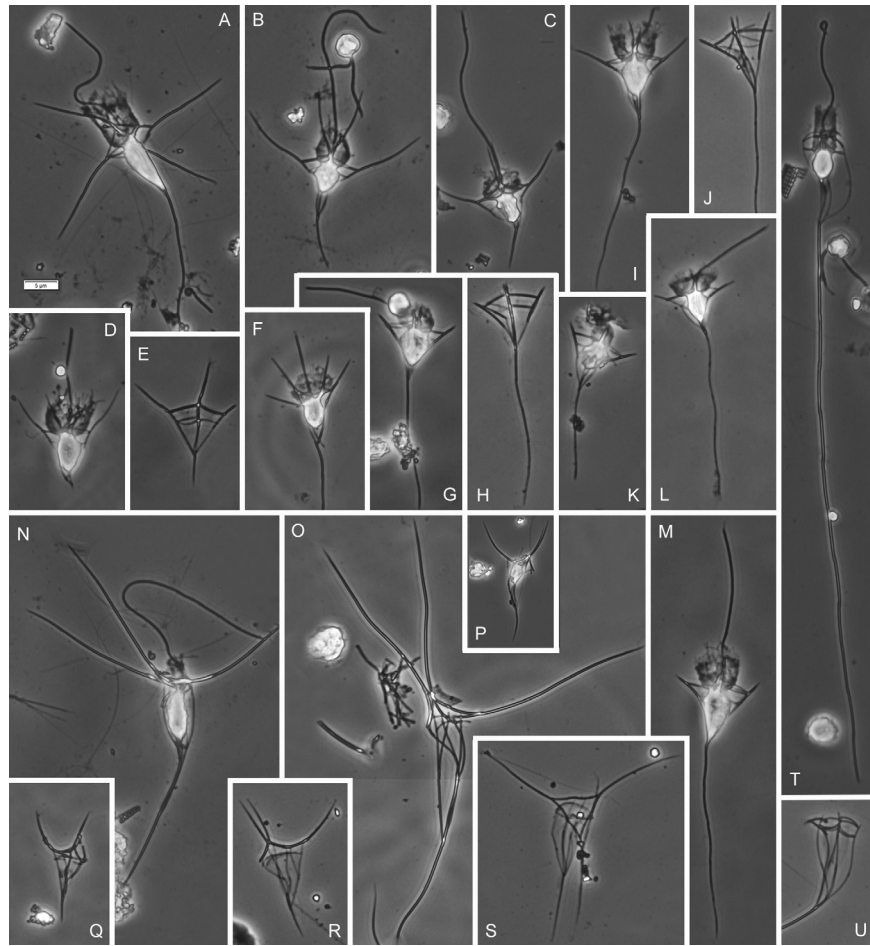


Fig. 28. *Calliakantha* spp. **A-F:** *Calliakantha simplex* from NOW (A, C, E), NEW (B, F), and Disko Bay (D) showing significant size variability. **G-M:** *Calliakantha simplex* cfr. from NEW (G, M), NOW (H-J, L), and Disko Bay (K). **N-S:** *Calliakantha natans* from NOW (N, Q) and Disko Bay (O-P, R-S) displaying also a remarkable size variability. **T-U:** *Calliakantha longicaudata* from NOW. The scale bar (A) applies to all LM images.

latitudes, and here only from the sub-arctic Disko Bay (Table 1). Despite its modest dimensions, it is easily recognized also in the LM. The conical minute lorica, the anteriorly protruding longitudinal costae, and the flagellum which reaches far beyond the lorica are the critical diagnostic features. The West Greenland material (Fig. 26) deviates from previously examined cells (Thomsen, 1988) in having significantly longer and sharply pointed anterior spines.

3.5.2.4. *Bicosta/Calliakantha* theme

The presence (Figs. 27, 28, 29, 30, 31) of long attenuated spines at both lorica ends is a typical feature of this cluster of taxa that are most abundantly present in the oceanic pelagic habitats.

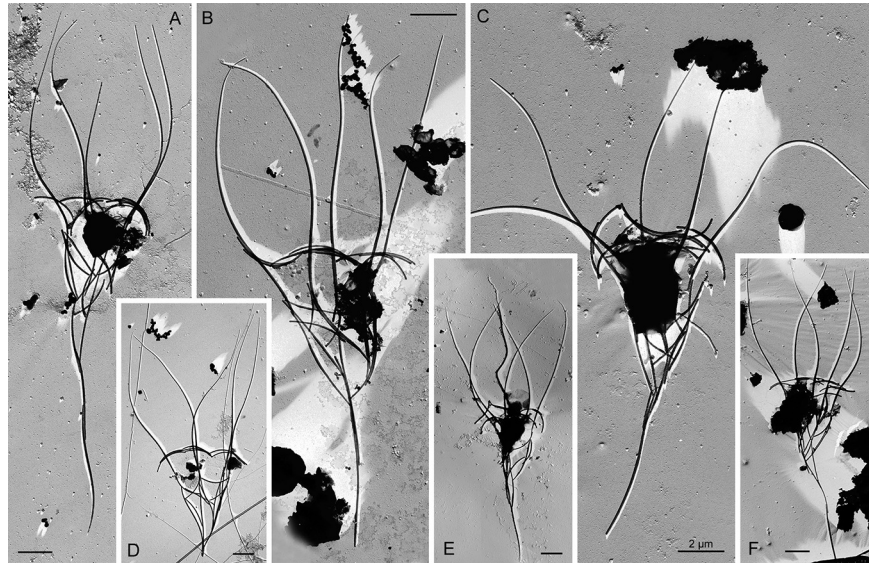


Fig. 29. *Saroecca attenuata* TEM specimens from Disko Bay 1977 (D) and 1990 (A-C, E-F). All specimens have five longitudinal costae and no indication of a well-defined second transverse costa.

3.5.2.4.1. Bicosta

Leadbeater, 1978 (Fig. 27) This genus currently encompasses three species, viz. *B. antennigera* (Fig. 27 A-L), *B. minor* (Fig. 27M), and *B. spinifera* (Fig. 27N) which are all prevalent in Arctic and sub-Arctic waters (Table 1 and Fig. 2) but also present in lower latitude samples (Fig. 3). The lorica is in all three species composed of 7 costal strips that represent two longitudinal costae with projecting spines anteriorly and a posterior pedicel. In *B. spinifera* and *B. minor* the lorica

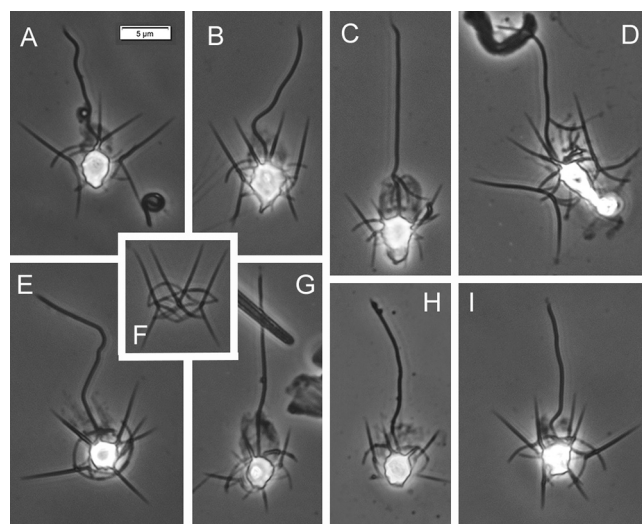


Fig. 30. *Spinoeca buckii* from NEW (A-C, F, H), NOW (D-E, G, I). The scale bar (A) applies to all LM images.

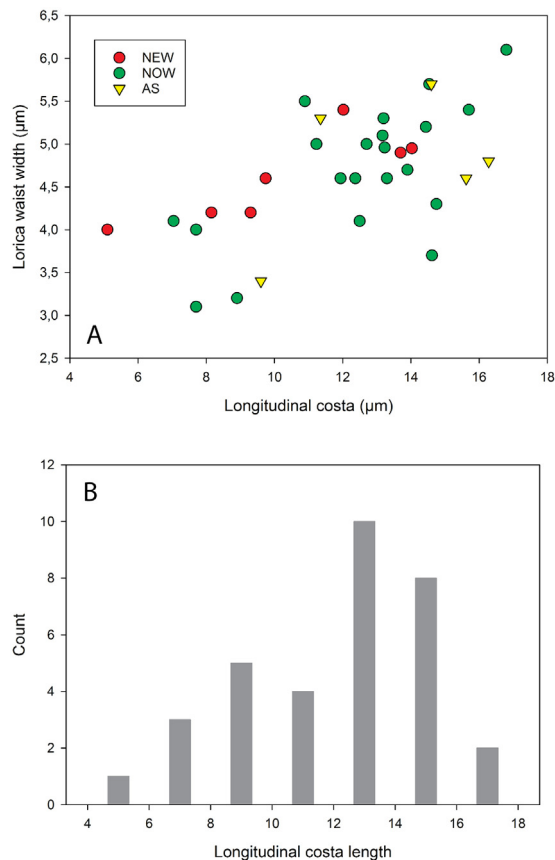


Fig. 31. *Spinoeca buckii* size variability across the regions sampled (A) with the indication of a weak bimodal distribution (B) of the specimens analyzed.

chamber is formed by 4 costal strips that in *B. spinifera* has a very conspicuous twist. In *B. antennigera* the lorica chamber is formed by just two costal strips while the other two strips become integrated in the anterior spines.

Dramatic size differences involving conspicuous bimodal patterns have already been demonstrated for *B. spinifera* (Thomsen and Larsen, 1992). Here we provide evidence for a similar morphological variability within *B. antennigera* (Fig. 27A–L). While *B. antennigera* specimens adhering to morphological characteristics as observed in the type material from New Zealand (Moestrup, 1979) here range in size from roughly 60–100 μm when measured along the contours of the lorica, the smaller *B. antennigera* specimens that are basically constructed according to the same principle, yet with a more stiff appearance of the lorica and slightly modified relative lengths of the elements, measure only 12–30 μm. When dealing with *B. spinifera* Thomsen and Larsen (1992) observed small specimens that prepared themselves for a sudden dramatic increase in lorica dimensions. This was evident from the presence of an extended ‘tail’ allowing for the production of new costal strips matching the demands of the large sized lorica (Thomsen and Larsen, 1992;

loc. cit. Figs. 24–25). A similar decisive proof of a size change over the time span of just one generation is not available with respect to *B. antennigera*. However, the overall appearance of the small sized versions of *B. antennigera* is convincingly similar to what was previously observed within *B. spinifera* (Thomsen and Larsen, 1992) leaving no doubt about that we are here looking at exactly the same phenomenon, and that we have just not managed to sample under environmental conditions that trigger the size change. The two size versions of *B. antennigera* often occur at the very same localities. As yet it has not been possible to deduct any repetitive patterns behind the occurrences.

The vast majority of the *B. spinifera* cells observed are large individuals similar to Fig. 27N. This specimen is 110 μm long when measured along the contours of the lorica.

Bicosta minor is by nature a much smaller species (Fig. 27M). Reynolds (1976) describing *B. minor* from the Barents Sea observed specimens that ranged in size between 30–45 μm . Specimens collected from Disko Bay 1990 ranged in lorica length from 16.5–33.5 μm .

3.5.2.4.2. Calliicantha

Leadbeater, 1978 (Fig. 28) Three species of *Calliicantha*, viz. *C. natans*, *C. simplex* and *C. longicaudata*, occur at all sites investigated here and are found everywhere to be among the community dominant species (Table 1 and Fig. 2). The genus is characterized by a fairly simple conical lorica chamber with two anteriorly positioned transverse costae and longitudinal costae that protrude anteriorly as short (*C. longicaudata*) or long spines (3 in *C. natans*/4 in *C. simplex*). Posteriorly the lorica carries either a spine (one costal strip) or as in *C. longicaudata* a stalk that comprises in excess of 10 costal strips.

Both *C. simplex* (Fig. 28A–E) and *C. natans* (Fig. 28N–S) occur at all sites sampled with two distinct morphotypes differentiated by overall lorica size and minor changes in the relative sizes of individual costal strips. In small specimens, the lorica chamber only diminishes to a small extent while the anterior and posterior projections are much more reduced (compare e.g. Fig. 28B and E (*C. simplex*) and Fig. 28O and R (*C. natans*)).

Calliicantha longicaudata specimens do vary in size within the same locality and when comparing material from different regions. However, dwarf-like specimens similar to those associated with both *C. natans* and *C. simplex* have not been observed so far.

The Greenland material additionally comprised specimens (Fig. 28G–M) that resemble *C. simplex* in having 4 longitudinal costae. However, these specimens lack the long protruding spines of *C. simplex* (one costal strip missing in each) and

has on the other hand a posterior projection that comprises up to 6 costal strips. In empty loricae (Fig. 28H, J) it appears that costal strips from the posterior transverse costa are somewhat irregularly positioned. The morphological and dimensional consistency in the appearance of this form across the three major sites sampled likely rules out the possibility that these are just cells of *C. simplex* damaged during the cell preparation. The presence of a posterior pedicel that deviates substantially from what is found in *C. simplex* sensu stricto adds yet another solid argument in favour of treating this form as a separate taxon. Long-stalked specimens have previously been reported by Thomsen et al., 1991b and by Tong (1997b), yet here with no change in the appearance of the anterior spines.

3.5.2.4.3. *Saroeca*

Thomsen, 1979 (Fig. 29) *Saroeca attenuata* has been found at several Arctic sites (Table 1). The genus was described based on material from the Baltic Sea (Thomsen 1979/*S. attenuata*). A second species, *S. paucicostata*, was later added by Hara and Takahashi (1987) and distinguished based on a reduced number of longitudinal costae and the presence of two transverse costae. While the existence of a second morphotype with a reduced number of longitudinal costae (4–5 versus 7–8 in *S. attenuata*) is unequivocal the case of the second transverse costa is less trivial. The illustrations accompanying the description of *S. paucicostata* (Hara and Takahashi, 1987) do not clearly demonstrate a second transverse costa because details are obscured by the presence of a protoplast. However, empty loricae from other warm water regions (e.g. the Andaman Sea, Indian Ocean) have been found (Thomsen, unpublished) that unambiguously support the description of this second species of *Saroeca*. The question is whether the cells that occur in Greenland waters should be identified as *S. paucicostata* as suggested by Hara and Takahashi (1987) with reference to the single Disko Bay specimen observed by (Thomsen, 1982, here reproduced as Fig. 29D). In this empty lorica there are admittedly costal strip patterns that may be interpreted as a second transverse costa. However, bifurcations of certain longitudinal costae followed by amalgamation of these or other longitudinal costae remains a valid alternative, in particular also because none of the costal strips involved are genuinely perpendicular to the longitudinal

Table 8. *Saroeca attenuata* – variability in the number of longitudinal costae.

<i>Saroeca attenuata</i>	Number of longitudinal costae					Observations	Source
	4	5	6	7	8		
Disko Bay, West Greenland	3	23	1			27	Østergaard, 1993
Baltic Sea(Finland, Denmark)			7	8	2	17	Thomsen, 1979

axis of the lorica but rather tilted. It is evident from Fig. 29A–C, E–F that Disko Bay loricae encountered during the 1990 field campaign are basically identical to the specimen illustrated by Thomsen (1982). For the time being we prefer to expand the *S. attenuata* species description to accommodate also loricae with 4–5 longitudinal costae and confine the use of the species epithet *S. paucicostata* to cases, so far exclusively from warm water regions, where the posterior transverse costa is well defined. Table 8 summarizes information on the numerical variability encountered in Baltic Sea and Disko Bay material.

3.5.2.4.4. Spinoeca

Thomsen et al., 1995 (Fig. 30) *Spinoeca buckii* (Fig. 30A–I) was particularly abundant in both polynya (Fig. 2). The lorica consists of four longitudinal costae (2 costal strips each) that project as free spines at both ends of the lorica. They are anteriorly connected by a single transverse costa and posteriorly by a meshwork of costal strips that also support the protoplast. There is a significant size variability which is evident when plotting across the three major sampling sites the length of a longitudinal costa versus the waist width of the lorica (Fig. 31A) which is suggesting a bimodal size distribution (Fig. 31B).

4. Conclusions

There is a great deal of homogeneity in species diversity and relative abundance when comparing the three sites sampled along the Greenlandic coastline (Figs. 2–3).

Robust ecological patterns emerge from the community analyses performed using Primer software features such as the shade matrix wizard and their PCA and MDA tools. Specific recurrent clusters of species are thus observed across the geographical areas sampled and these are furthermore found to be most likely associated to nutrient deprived versus nutrient replenished habitats.

Bimodal size distributions are common among loricate choanoflagellate species and previously documented from e.g. *Bicosta spinifera* (Thomsen et al., 1990; Thomsen and Larsen, 1992), *Calliakantha natans* (Thomsen, 1982; Thomsen et al., 1990), *C. simplex* (Thomsen et al., 1990), *Parvicorbicula socialis* (Manton et al., 1976), and *P. circularis* (Thomsen et al., 1990). Here we have added some additional cases, i.e. *Bicosta antennigera*, *Parvicorbicula manubriata*, *P. quadricostata*, and *Spinoeca buckii*, and corroborated previous observations with respect to *Calliakantha natans*, *C. simplex*, *Cosmoeca ventricosa*, and *Parvicorbicula socialis*. We have at present no explanation that can convincingly illuminate the causes behind the observed bimodal size distributions. However, we are inclined to believe that what we are observing is likely the manifestations of

distinguishable loricate choanoflagellate morphotypes forming part of an as yet unresolved asexual or sexual life history controlled by environmental clues.

Establishing molecular barcodes for diverse choanoflagellate species will provide a permanent link between their morphology and their genomes, and will immediately allow us to use their barcodes as queries in burgeoning sequence databases to understand both their world-wide distribution and perhaps also help unravelling the possible loricate choanoflagellate life histories hinted at above. The current analysis of choanoflagellate species occurrences and relative abundances in Greenlandic waters serves several purposes. On the one hand and considering the fact that loricate choanoflagellates can be recognized light microscopically it does serve as a historical base-line study of these organisms that will allow a future tracking of community changes in parallel with climate change ecosystem impacts. On the other hand, the level of details presented here will also critically support future attempts to sequence additional species. In all probability, the key to success here will be single cell isolation of species from a concentrated natural sample (see e.g. Nitsche et al., 2017). A profound knowledge of the species and morphotypes that are likely to occur is a key element in quality assuring this procedure.

Declarations

Author contribution statement

Helge Thomsen: Conceived and designed the experiments; Performed the experiments; Analyzed and interpreted the data; Contributed reagents, materials, analysis tools or data; Wrote the paper.

Jette Østergaard: Conceived and designed the experiments; Performed the experiments; Analyzed and interpreted the data.

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Competing interest statement

The authors declare no conflict of interest.

Additional information

No additional information is available for this paper.

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